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GABBRO SOIL-PLANT RELATIONS IN THE CALIFORNIA FLORISTIC PROVINCE

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Abstract

The paper reviews published botanical and pedological literature concerning gabbro in the California Floristic Province. Gabbro is a mafic plutonic rock that is common in the Sierra Nevada, Klamath Mountains, and Peninsular Ranges of the California Floristic Province. Its mineralogical and chemical compositions span the range between those of peridotite, an ultramafic rock, and diorite, a rock more silicic than gabbro. A broad range of nutrient element compositions makes gabbro soils extremely diverse substrates that harbor numerous rare and endemic plant species, particularly at the Pine Hill intrusive complex in El Dorado County, California. Several directions for further work are also suggested. More research is required to discern the poorly understood factors affecting endemism and plant distributions on gabbro soils. Attention should be paid to floristic differences between olivine gabbro, which chemically borders serpentine, and gabbro lacking olivine or containing more hornblende than olivine. A species list is provided which highlights rare, serpentine-preferring, and gabbro-endemic taxa reported from gabbro soils in the California Floristic Province.

Key Words: Edaphic endemism, gabbro, geobotany, plant nutrition, plant-soil relations, rare plants, soil chemistry.

Soil is an intermediary between bedrock and vegetation. The chemical composition of this biologically important layer is largely determined by the composition of underlying parent materials (Rajakaruna and Boyd 2008). Soil composition is a significant factor in plant ecology and evolution: various plant species have evolved specific traits, such as the ability to tolerate heavy metals or nutrient imbalances, as a result of natural selection in populations on particular soils (Kruckeberg 1986; O'Dell and Rajakaruna 2011). These traits influence plant physiology, distribution, and speciation, demonstrating that attention to soil parent materials is a vital part of botanical research. While certain edaphic systems, such as serpentine (Harrison and Rajakaruna 2011) and gypsum (Escudero et al. 2015; Moore et al. 2014), have been the subject of extensive study, gabbro has not received the same level of attention as a unique edaphic environment.

Gabbro is a mafic (magnesium- and iron-enriched) rock with mineralogy and chemistry that span the range between diorite and peridotite (Fig. 1). Gabbro soils develop from gabbro parent materials. They share many plant species with diorite soils and some with ultramafic soils (Whittaker 1960); several plant species characteristic of ultramafic soils are also found on gabbro soils (Baldwin et al. 2012). Worldwide, the distribution of plant species and communities on gabbro soils have been addressed by Gertenbach (1978) and Peel et al. (2007) in South Africa, Marrs and Proctor (1978) in England, Dayton (1966) in North Carolina, Schmidt and Barnwell (2002) in South Carolina, and Buck (1964) in Oklahoma. These studies have generally noted the existence of distinctive plant communities on gabbro soils, and have either offered no explanation or speculated that the unique assemblage of species is due to unusual nutrient levels or soil types. Other studies have used gabbro as a "normal" substrate to which the vegetation of a serpentine substrate is contrasted (e.g., Adamson et al. 1993). In the California Floristic Province (CFP), the vegetation of gabbro soils has been discussed by Whittaker (1960), Hunter and Horenstein (1992), Oberbauer (1993), Tarp (1998), Tarp et al. (2002), Wilson et al. (2010), Burge and Manos (2011), Gogol-Prokurat (2011), and others.

In this paper we review the published literature concerning rocks, soils, and plants of gabbro outcrops in the CFP. We provide descriptions of gabbro rocks and soils, followed by an overview

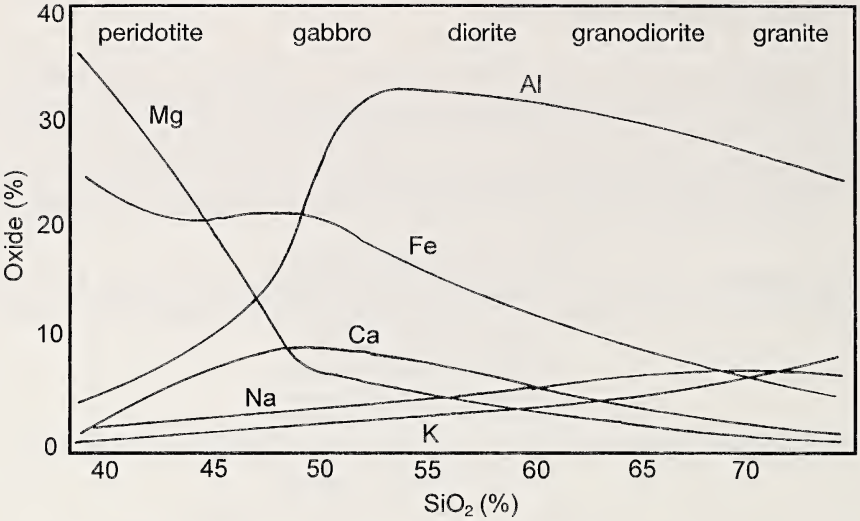

FIG. 1. Metal oxide concentrations in plutonic rocks, based on data in Le Maitre (1976).

of plant nutrition on gabbro soils. We then discuss hypotheses for the restriction of some taxa to gabbro soils and some possibilities for identifying the limiting properties of gabbro soils that might restrict the distributions of rare plants. Finally, we highlight gabbro areas in California where botanical research has been conducted, and provide a list of gabbro-endemic, rare, and otherwise interesting plants known to occur on gabbro in the CFP (Appendices 1 and 2).

Occurrence And Composition Of Gabbro

Gabbro is a plutonic igneous rock formed by the subterranean solidification of mafic magma. It is found in Precambrian layered complexes on continental platforms (e.g., the Canadian Shield), in more recent plutons in continental orogenic regions, and in the oceanic crust continuously produced at mid-ocean spreading centers. In the CFP, gabbro is widely distributed in Mesozoic plutons in the Sierra Nevada, Klamath Mountains, and Peninsular Ranges, and sparsely distributed in the eastern Transverse Ranges and the California Coast Ranges; gabbro also occurs in the western Mojave Desert, just outside the CFP (CGS 2010; Fig. 2).

Geologists characterize igneous rocks with regard to mineral composition and texture (Fig. 1). Chemically, gabbro is identical to basalt; unlike gabbro, basalt solidifies at the Earth's surface, cooling quickly to produce an aphanitic (small grained) texture. Gabbro has a phaneritic (large-grained) texture formed by the slow crystallization typical of plutonic rocks. It is composed predominantly of the minerals pyroxene, plagioclase that is more calcic (Ca-rich) than sodic (Na-rich), and either olivine or hornblende (Le Maitre 2002; Table 1). Olivine is a Fe-bearing Mg-silicate, while hornblende is a silicate mineral containing Ca, Al, and Na in addition to Fe and Mg. Gabbro generally contains more clinopyroxenes (containing Ca) than orthopyroxenes (lacking Ca); the closely related rock norite is fundamentally gabbro dominated by orthopyroxenes. Silica (SiO_2) content in gabbro ranges from around 45% to about 54%; aluminum (Al) and magnesium (Mg) contents vary considerably in this range (Fig. 1), suggesting that broad ranges of these elements can be expected in gabbro rocks. And the range of possible chemical compositions is much broader for gabbro with olivine than for gabbro with hornblende (Alexander 2011). It is therefore inappropriate to assume that a gabbro outcrop or soil will conform to a generalized composition. Mineral contents or elemental concentrations must be measured at each gabbro site under study to be relevant to that site.

Gabbro Soils

A brief note concerning terminology is warranted here. Although "gabbroic soils" would be a better term grammatically, we use the phrase "gabbro soils" here to be consistent with other geoecological literature, in which "serpentine soils" is the accepted term for soils derived from serpentinite and other related rocks (see Rajakaruna et al. 2009).

Gabbro soils contain minerals inherited from their gabbro parent materials, and as a consequence are as diverse as the gabbro rocks discussed above. This diversity is compounded by the effects that climate, vegetation, exposure time, and topography may exert on soil formation (Kruckeberg 1986). For example, gabbro soils in the colder climate of the Klamath

FIG. 2. Gabbro distribution in the California Floristic Province (CFP). Approximate border of CFP shown by bold line; note that it includes parts of California, Oregon, and Baja California. Geographic abbreviations: GC, Gulf of California; KM, Klamath Mountains; OCR, Oregon Coast Ranges; SN, Sierra Nevada; TR, Transverse Ranges. The following gabbro outcrops discussed in this paper are marked with an approximate position on the map: a, Pine Hill Intrusive Complex; b, Guatay Mountain and King Creek Research Natural Areas, c, Klamath-Siskiyou Mountains; d, Bodfish Piute Cypress Botanical Area. Map based on Gastil (1975), Jennings (1977), and Walker and McLeod (1991).

Mountains typically have less clay than gabbro soils in the warmer Peninsular Ranges (EBA, unpublished data).

Gabbro soils in the CFP are mostly Alfisols, with some Inceptisols and Mollisols, and a few Entisols (Soil Survey 1973; Soil Survey Staff 1999). They are in loamy-skeletal, fine-loamy, clayey-skeletal, and fine families. Unlike granite, gabbro typically weathers to silt and clay rather than coarse grus. Therefore, gabbro soils are commonly less sandy and more silty and clayey than granite soils (Alexander 1993). Because gabbro is generally more Fe-rich than granitic rocks, gabbro soils are commonly redder than

TABLE 1. MAJOR MINERALS IN INTRUSIVE IGNEOUS ROCKS, FROM DOMINANT (+++) TO MINOR (+), OR ABSENT (—). Both extrusive volcanic and chemically equivalent intrusive plutonic rocks have the same, or similar, minerals; it is mainly the grain sizes that are different. [a] The major cations in alkali feldspars are Na and/or K. [b] Hornblende is a major element in hornblende gabbro, but a minor element in olivine gabbro. Data compiled from Le Maitre (2002).

Mineral	Peridotite	Gabbro	Diorite	Granodiorite	Granite
Quartz	—	—	—	++	+++
Alkali Feldspars[a]	—	—	+	++	+++
Calcic Feldspars	—	+++	++	+	—
Biotite	—	—	—	+	++
Hornblende[b]	—	+	+++	++	+
Pyroxenes	+++	++	+	—	—
Olivine	+++	+	—	—	—

granite soils. Granite soils that are reddish are more yellowish red, while gabbro soils are more brownish red. Gabbro has more basic cations, especially Ca and Mg, than granitic rocks, and commonly less Al (except gabbro with much hornblende or feldspar); consequently, the cation-exchange complexes of gabbro soils generally have larger percentages of basic cations (greater base saturation) than the cation-exchange complexes of granitic soils. Soil pH is commonly higher in gabbro soils than in granite soils, mainly because base saturation is commonly higher in the former. Gabbro soils in the CFP are most commonly slightly to moderately acidic (Soil Survey 1973; Alexander 2011).

Gabbro soils differ from ultramafic soils (such as soils derived from serpentine) in having more Ca and much less Mg, as reflected in molar Ca/Mg ratios >> 1 in surface soils and > 1 in subsoils (Alexander 2011), whereas the ratios in serpentine soils are generally < 1 in surface soils and << 1 in subsoils (Alexander et al. 2007). First transition elements that can be toxic to plants (Cr, Co, and Ni) are much less concentrated in gabbro soils than in serpentine soils (Table 2). Nevertheless, some soils developed from olivine gabbro may have elemental concentrations nearer to those of serpentine soils than to average gabbro soils. Serpentine soils are known to be harsh environments with high rates of endemism (Safford et al. 2005; Anacker 2011), so understanding the similarities between serpentine soils and gabbro soils may help us better understand gabbro endemism.

TABLE 2. FIRST TRANSITION ELEMENTS (ATOMIC NUMBERS 21–30) AND MOLYBDENUM (MO) IN IGNEOUS ROCKS FROM WORLDWIDE AVERAGES OF VINOGRADOV (1962), WHO INCLUDED ANDESITE WITH DIORITE, BASALT WITH GABBRO, AND DUNITE WITH PERIDOTITE.

Element	Diorite concentration (ppm)	Gabbro concentration (ppm)	Peridotite concentration (ppm)
Sc	2	24	5
Ti	8000	9000	300
V	100	200	40
Cr	50	200	2000
Mn	1200	2000	1500
Fe	58,500	85,600	98,500
Co	10	45	200
Ni	55	160	2000
Cu	35	100	20
Zn	72	130	30
Mo	0.3	1.4	0.9

PLANT NUTRITION IN GABBRO SOILS

Plants require C, H, O, N, and K in large amounts, Ca, Mg, P, S, Cl, Fe, B, and Mn in moderate amounts, Cu, Na, and Zn, in small amounts, and Mo, Co, and Ni in minute amounts for their growth (Marschner 1995). Several of these elements pertain directly to gabbro soils and are discussed below.

Nitrogen that plants acquire as NO_3^- must be reduced to NH_4^+ with nitrogen reductase, an enzyme containing Mo. Although Mo has been reported to limit plant growth in serpentine soils (Walker 1948; Alexander et al. 2007), there is no research suggesting that it is a limiting element in gabbro soils. According to Vinogradov (1962), the average content of Mo in gabbro is significantly greater than that of ultramafic rocks or diorite. However, as stated previously, average values have little significance for individual gabbro outcrops, and we know of no data on the variability of Mo contents in gabbro across California.

Average Ca contents are high in gabbro compared to more silicic igneous rocks (Table 2, Fig. 1), but the range in compositions varies greatly. Whereas molar exchangeable Ca/Mg ratios in olivine gabbro soils may be so low (possibly <0.7) that plants may be unable to uptake sufficient Ca, the exchangeable Ca/Mg ratios in hornblende gabbro soils may be so high that plants cannot obtain sufficient Mg.

Potassium exists at low concentrations in gabbro parent material (Le Maitre 1976). In an investigation of three gabbro soils in the Pine Hill area of the Sierra Nevada and three in the Cuyamaca-Guatay area of the Peninsular Ranges (Alexander 2011), the Pine Hill soils contained

less K than the Cuyamaca-Guatay soils. The Cuyamaca-Guatay soils had parent materials with considerable hornblende, which is a potential source of K, whereas the Pine Hill soil parent materials were replete with pyroxenes that lack K.

Phosphorus is typically low in plutonic rocks (Le Maitre 1976), and may be particularly low in gabbro (Barral et al. 2011). Dust from the atmosphere may be a major source of P in gabbro soils, just as proposed for serpentine soils (Alexander et al. 2007). Phosphorus derived from the weathering of soil parent material or from dust is utilized by plants and accumulates in soil organic matter. Plants continuously recycle it and little is lost from undisturbed soils. Alexander (2011) showed that the amounts of P in gabbro soils of the Pine Hill and Cuyamaca-Guatay areas are related to amounts of soil organic matter. The bioavailability of soil P is closely related to soil pH, with P fixed as Ca-phosphates at high pH and adsorbed on Fe and Al-oxides at low pH (Frossard et al. 1995). The pH values of gabbro soils in the CFP are generally in or near the 6 to 7 range (Soil Survey 1973) where soil P is most available to plants (as mono- or di-hydrogen phosphates; Frossard et al. 1995). Available P varies seasonally along with microbial activity and plant uptake (Sharpley 2000); measured values of "available" P may also depend heavily on the type of extraction used.

Sulfur occurs in minute amounts in gabbro (about 0.3 g/kg in mafic rocks according to Vinogradov 1962), mainly in sulfides such as pyrite (FeS_2). Most of the S in gabbro soils is deposited from atmospheric gasses and from sulfates in precipitation. The major sources of atmospheric S are volcanic activity and the burning of fossil fuels and vegetation. Plants do not require much S and it is recycled back into plants as sulfates from the decomposition of plant detritus. Sulfur is more mobile than P in soils and deficiencies can occur in highly leached soils (Marschner 1995), but S deficiencies are unlikely to occur in gabbro soils of the CFP (Alexander 2007; but see Burge and Manos 2011).

Copper, Mn, and Zn contents in gabbro are higher than the contents in other kinds of plutonic rocks, and like other mafic and ultramafic rocks gabbro contains ample amounts of Fe, Co, Ni, and Mg (Table 2). No plant nutrient deficiencies would be expected for these elements in gabbro soils or for other micronutrients such as Cl, B, and Na.

To summarize the soil elemental data: K is low in some gabbro soils and may be a limiting nutrient, but this varies within and between soils or outcrops. P may be a limiting nutrient, depending on the pH of the site. Bioavailability of Ca and Mg varies with the type of gabbro. Other nutrients do not seem to be scarce in gabbro soils, and although the concentrations of some micronutrients are higher in gabbro than in other plutonic rocks, metal toxicity does not seem to be an issue.

The Edaphic Factor In Plant Distributions On Gabbro Soils

Various authors have cited soil nutrient levels, soil moisture, slope position, slope aspect, and other factors as being important in the distributions of plants within an area of gabbro soil. Some of these factors are discussed below; which factor is most important almost certainly depends on the particular species in question.

Gabbro soils that support rare plants exhibit a broad range of physical characteristics; similar ranges of physical characteristics are found in many Alfisols and Mollisols of California with other parent materials (Soil Survey 1973). It has therefore been assumed that soil chemistry, rather than physical characteristics, is responsible for unique plant associations found on gabbro soils. This assumption was implicit in Hunter and Horenstein (1992) and other references cited in the introduction. However, Alexander (2011) found that adjacent gabbro soils, which supported or lacked rare plants at the Pine Hill and Cuyamaca-Guatay areas, did not differ significantly in important plant nutrients such as K and P.

There is great variation in the chemistry of soils derived from gabbro, and plant distributions on gabbro soils are likely dependent on more than soil chemistry (Gogol-Prokurat 2011). Wilson et al. (2010) investigated the distributions of eight rare plant species on gabbro in the Pine Hill area of El Dorado County, and all but one of those species occurred in different plant communities and microclimates. They suggested that slope aspect was one of the key factors affecting the distribution of these species. Two of the Pine Hill species, *Calystegia stebbinsii* Brummitt (Convolvulaceae) and *Packera layneae* (Greene) W.A. Weber & A. Löve (Asteraceae), occur on both gabbro and serpentine soils, but on no soils with other parent materials. Another plant that grows only on gabbro and serpentine soils in the Klamath Mountains is *Frangula californica* (Eschsch.) A. Gray subsp. *occidentalis* (Howell ex Greene) Kartesz & Gandhi (Rhamnaceae) (Alexander 2014).

Another intriguing phenomenon is the occurrence of plants on some gabbro soils but not on nearby gabbro soils with similar microclimates; this problem of distribution was addressed by Burge and Manos (2011, but also see Alexander 2012). Distributions of certain rare plants are spotty even on the same kinds of gabbro soils, and many of the same rare plants appear on diverse kinds of gabbro soils. In San Diego County, for example, *Hesperocyparis stephensonii*

(C.B. Wolf) Bartel (Cupressaceae) was found on both a brown Alfisol (Haploxeralf) and a red Alfisol (Rhodoxeralf) with gabbro parent materials (Alexander 2011). Considerably lower exchangeable Ca in the brown Alfisol may be more of a limitation for the cypress than the physical characteristics that differentiate between the Haploxeralf and Rhodoxeralf great groups. The focus of geobotanical investigations should be on soil properties rather than on soil classification.

Burge and Manos (2011) suggested that the gabbro endemic *Ceanothus roderickii* W. Knight evolved from a population of *C. cuneatus* (Hook.) Nutt. var. *cuneatus* that was locally adapted to nutrient-poor gabbro soils in the Pine Hill area. They noted that *C. roderickii* is generally found on steeper slopes with less developed soil, while *C. cuneatus* var. *cuneatus* is predominantly found near slope bottoms. It is still not clear why *C. roderickii* or many of the other Pine Hill endemics remain restricted to gabbro alone.

In terms of strict endemism, there are fewer than 10 gabbro endemics in California. The gabbro-endemic taxa at Pine Hill and elsewhere (Appendix 1) comprise a tree, shrubs, and forbs; many come from high-diversity genera in the CFP flora (e.g., *Ceanothus* L.), while others do not (e.g., *Wyethia* Nutt.). They are all perennials (Baldwin et al. 2012); they are probably all neoendemics (Harrison 2014). Further study of the age and edaphic tolerances of these species will be required before any definite statements can be made about gabbro endemism or other unusual plant distributions seen on gabbro soils.

On The Relationship Between Plant Distribution On Gabbro And Serpentine Soils

As we have mentioned previously, chemical and mineralogical similarities exist between gabbro (particularly olivine gabbro) and serpentine. Furthermore, the two rock types are often found in close proximity (Alexander et al. 2007; Lyons et al. 2010; Wilson et al. 2010). As discussed elsewhere in this paper, certain "gabbro endemics" have been reported from nearby serpentine sites, and vice versa for "serpentine endemics" on gabbro. This leads to an as-of-yet unresolved question: are certain serpentine endemics found on gabbro because it is sufficiently similar to serpentine in chemistry, nutrition, ecological competition, or some other factor to allow limited colonization, or are the taxa in question not "endemic" to serpentine at all, but to some feature shared between the two substrate types?

Because gabbro produces soils that are less "harsh" than serpentine soils, it makes sense that serpentine endemism is a more dramatic (and prevalent) phenomenon than gabbro endemism. But since olivine gabbro is chemically somewhat similar to serpentine, vegetation similarities might be expected between the two; likewise, fewer vegetation similarities would be expected between hornblende gabbro and serpentine. These areas need further study before conclusions can be reached on the relationship between plant distribution patterns on gabbro and serpentine soils.

Notable Gabbro Outcrops In The California Floristic Province

Bodfish Piute Cypress Botanical Area

This protected area in Sequoia National Forest is located south of Lake Isabella in Kern County. Gabbro soils at this site support *Streptanthus cordatus* Nutt. var. *piutensis* J. T. Howell (Brassicaceae), a rare plant known only from Kern County (Greene and Sanders 1998). This taxon has not been labeled a strict gabbro endemic, as a few individuals have been reported from off gabbro. However, considering that most *Streptanthus* Nutt. spp. exhibit some degree of serpentine affinity (Baldwin et al. 2012), it would not be inconceivable for *S. cordatus* Nutt. var. *piutensis* to be a gabbro endemic. This taxon requires more thorough geoecological study.

Guatay Mountain and King Creek Research Natural Areas

Areas of hornblende gabbro are located in San Diego County, California, within Cleveland National Forest. They were investigated (as the "Cuyamaca-Guatay area") by Alexander (2011). *Hesperocyparis stephensonii,* a gabbro-endemic conifer, occurs only at the King Creek site, and within that site is restricted to the deeper, wetter soils at the base of slopes, rather than drier, steeper soils further upslope (Keeler-Wolf 1990). The Viejas Mountain Research Natural Area, another incidence of gabbro soil in Cleveland National Forest known to support at least one rare plant species (USFS s.d.), was not included in Alexander's 2011 study. Species lists for all three areas have been compiled in unpublished Forest Service reports.

Pine Hill Preserve

Located in El Dorado County in the Sierra Nevada foothills, the Pine Hill Preserve has received considerable attention from California botanists and soil scientists (see Hunter and Horenstein 1992; Wilson et al. 2010; Alexander 2011; Burge and Manos 2011). A comprehensive survey of the area (Wilson et al. 2010) lists 741 vascular plant taxa, of which 634 taxa occur on the preserve's olivine gabbro. These include two species – *Quercus durata* Jeps. and *Streptanthus*

polygaloides A. Gray – that are described as narrow or strict serpentine endemics (Safford et al. 2005). *Chlorogalum grandiflorum* Hoover (a broad serpentine endemic) and *Packera layneae* (a strong serpentine indicator) also grow on gabbro at Pine Hill.

Several species are endemic to this area, including *Calystegia stebbinsii, Ceanothus roderickii, Fremontodendron decumbens* R. M. Lloyd, *Galium californicum* Hook. & Arn. subsp. *sierrae* Dempster & Stebbins, and *Wyethia reticulata* Greene (Brummitt 1974; Hunter and Horenstein 1992; Ayres and Ryan 1999; Wilson et al. 2010). For discussions of the fire and dispersal ecology of *F. californicum* subsp. *decumbens* and *C. roderickii,* see Boyd and Serafini (1992) and Boyd (1994, 1996, 2001, 2007). For genetic information on the two aforementioned species and *W. reticulata,* see Ayres and Ryan (1999), Kelman et al. (2006) and Burge and Manos (2011). It is not clear why the Pine Hill site harbors most of California's gabbro endemics, although habitat complexity has been suggested as a possible reason.

It would be tempting to ascribe the greater number of serpentine indicator plants observed by Alexander (2011) at Pine Hill versus the Guatay Mountain and King Creek RNAs to the presence of olivine gabbro (which is chemically closer to serpentinite) at Pine Hill versus the presence of hornblende gabbro at Guatay Mountain and King Creek. However, the Pine Hill intrusive complex contains a perimeter of ultramafic rocks around the gabbroic pluton, while the Guatay Mountain and King Creek areas do not (CGS 2010). Further work is needed to isolate substrate effects on distribution from dispersal effects on distribution.

Diablo Range

In a floristic report of the Mount Hamilton region of the San Francisco Bay Area, Sharsmith (1945) said very little about gabbro, reporting only that soils derived from gabbro are infertile. We presume that she was referring to a small gabbro outcrop near what is now Frank Raines Regional Park, an off-highway vehicle area, since there are no other gabbro outcrops near Mount Hamilton (CGS 2010). This outcrop is adjacent to a much larger area of serpentine, and could be an interesting site in which to compare the vegetation of the two parent materials.

Klamath-Siskiyou Mountains

Whittaker (1960) investigated plant distributions along a moisture gradient on diorite, gabbro, and serpentine soils in northern California and southern Oregon, emphasizing the individuality of species' responses to different soils and describing gabbro plant communities that were intermediate between those of granitic and ultramafic soils. He reported that gabbro forests were more open and less dominated by *Pseudotsuga menziesii* (Mirb.) Franco than nearby diorite forests, and that stream banks were more vegetated on gabbro than on either serpentine or diorite; however, a later analysis of his data by Grace et al. (2011) found that overall species richness was lowest on gabbro. Several species were mostly absent on diorite but were major elements of gabbro communities: *Umbellularia californica* (Hook. & Arn.) Nutt. (which also occurs at Pine Hill [Wilson et al. 2009]), *Arctostaphylos cinerea* Howell, *Frangula californica* subsp. *occidentalis* (Howell) Kartesz & Gandhi, and *Vaccinium ovatum* Pursh. Four species were found on gabbro only: *Luina hypoleuca* Benth., *Darmera peltata* (Torrey) Voss, *Epipactis gigantea* Hook., and *Erigeron cervinus* E. Greene. Damschen et al. (2010) resurveyed Whittaker's serpentine and diorite sites and documented a loss of species diversity, especially endemic species diversity; they ascribed this shift to climate change. Whittaker's gabbro sites were not resurveyed because a 2002 fire burned the entire gabbro study area.

Future Directions

The first step towards identifying soil properties responsible for selective distributions of plants on some gabbro soils and not on others would be to comprehensively analyze many gabbro surface and subsoils with similar microclimates throughout an area. Analyses of both surface soils and subsoils sampled below 25 or 30 cm are important, to account for differences in rhizosphere depth between plant species. Surface soil properties can be influenced greatly by recent disturbance and differences in plant cover that may be unrelated to the properties of the soil as a whole. Following soil sampling and analyses, comparisons of the properties of soils supporting rare plants with the properties of soils lacking rare plants may provide some clues about those soil properties that limit the distributions of the plants.

Gabbro endemism in vascular plants is poorly studied in comparison to serpentine endemism. Reciprocal transplants and common garden studies with plants known only from gabbro could help to clarify the nature of gabbro endemism, provided that these studies examine a variety of variables such as soil type and structure, slope and aspect, and soil chemistry. Such studies should investigate whether purportedly gabbro endemic taxa can survive on serpentine or granite/diorite soils if given the opportunity. The reverse (whether serpentine endemics can survive on gabbro) should also be tested.

To the best of our knowledge no one has published a survey of bryophytes on gabbro outcrops in California. One such survey in South Carolina (Bowe and Rayner 1993) found moisture to be a more important factor than bedrock type in determining species composition. However, at least one rare moss species in California is endemic to serpentine: *Pseudoleskella serpentinensis* P. Wilson & Norris has been reported from serpentine in the Klamath-Siskiyou area (Malcolm et al. 2009). No comprehensive work has been done on the lichens of gabbro outcrops in California. As serpentine rocks in the CFP have been shown to support unique lichen assemblages (Rajakaruna et al. 2012), a study of gabbro lichens could be worthwhile. Comparisons should also be made between mycorrhizal communities on gabbro and other unique substrates, such as serpentine (Southworth et al. 2014).

Gervais and Shapiro (1999) discussed edaphic endemism (as a consequence of plant specificity) in Sierra Nevada Lepidoptera. They focused on serpentine, but did note populations of "serpentine endemic" butterflies and skippers on gabbro. Further entomological insight could follow from a better understanding of why certain plants live on certain gabbro soils.

In terms of conservation, work should be done to model the effects that climate change may have on the plants of gabbro soils, as has been done for serpentine (see Damschen et al. 2012). Other threats to these plants should also be regularly assessed. One could speculate that the plants restricted to gabbro soils face greater conservation threats than serpentine plants because gabbro lacks the public awareness that serpentine has earned as California's state rock.

Further work should be done to map the distributions of olivine and hornblende gabbro in the CFP, and to integrate this knowledge with research in gabbro vegetation ecology. Although endemism to particular rock types is a paradigm in geoecology, chemical variation can cause significant variation in vegetation within one "type" of rock (Hahm et al. 2014). Differences between the gabbro outcrops documented by Alexander (2011) may be attributable to rock chemistry differences, and we believe that this could be a fertile area of research in the future.

Conclusions

Although gabbro has not received as much attention as serpentine, it is a unique edaphic system that poses several interesting questions concerning endemism, species distributions, and edaphic ecology. Soil chemistry, soil moisture, topography, and proximity to serpentine bedrock may all play a role in the formation of a unique gabbro vegetation, although much more work remains to be done before gabbro endemism is understood on either a broad or a species-by-species basis. Continued research into the evolution and ecology of gabbro endemic taxa should be an important facet of geobotanical investigations in the California Floristic Province.

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Appendix 1. Rare Plants Reported from Gabbro Soils of the California Floristic Province

This appendix summarizes the taxa that have been (a) reported to occur on gabbro in the CFP, and (b) have a rarity status according to the California Native Plant Society and/or a serpentine indicator rating in Safford et al. (2005). An exhaustive search of California herbaria would almost certainly reveal additional taxa that belong on this list, although such a search is not within the scope of this paper (to that end, though, we encourage herbaria to make their online collections databases more easily searchable by ecological data).

Headings. Serp. = serpentine affinity as reported in Safford et al. (2005); CA = California listing status as reported in CNPS (2013); FE = federal listing status as reported in CNPS (2013); CNPS = rare plant rank as reported in CNPS (2013). Gabbro endemic taxa are in bold text; potential gabbro endemics are followed by a bold question mark in parentheses (**?**).

Literature sources indicate where each taxon is reported on gabbro: a. Alexander et al. 2007; b. Alexander (2011); c. Alexander (2014a); d. Ayres and Ryan (1999); e. Baldwin et al. (2012); f. Boyd and Ross 1997; g. Burge and Manos (2010); h. CNPS (2013); i. Greene and Sanders (1998); j. Simpson et al. 2013; k. Hirshberg and Levin 1988; l. Hunter and Horenstein 1992; m. Levin and Hirshberg 1991; n. Preston (2006b); o. USDA s.d.; p. Whittaker (1960); q. Beauchamp (1986).

				Rarity		
Family	Taxon	Source	Serp.	CA	FE	CNPS
Apiaceae						
	Lomatium howellii (S. Watson) Jeps.	p	6.1	-	-	4.3
Asteraceae						
	Arnica spathulata Greene	p	5.5	-	-	4.3
	Erigeron cervinus Greene	p	3.3	-	-	4.3
	Packera ganderi (T.M. Barkley & R.M. Beauch.) W.A. Weber & A. Löve	e	-	CR	-	1B.2
	Packera layneae (Greene) W.A. Weber & Á. Löve	b, l	4.9	CR	FT	1B.2
	***Wyethia reticulata* Greene**	b, d	-	-	-	1B.2
Boraginaceae						
	Cryptantha wigginsii I.M. Johnst.	j	-	-	-	1B.2
Brassicaceae						
	Sibaropsis hammittii S. Boyd & T.S. Ross	f				
	Streptanthus cordatus Nutt. var. *piutensis* J. T. Howell (**?**)	i	-	-	-	1B.2
Cistaceae						
	Crocanthemum suffrutescens (B. Schreib.) Sorrie	l	-	-	-	3.2
Convolvulaceae						
	***Calystegia stebbinsii* Brummitt**	l	-	CE	FE	1B.1
Crassulaceae						
	Sedum laxum (Britton) A. Berger subsp. *heckner*i (M. Peck) R.T. Clausen	e, g	3.5	-	-	4.3
Cupressaceae						
	Hesperocyparis forbesii (Jeps.) Bartel	b	-	-	-	1B.1
	Hesperocyparis nevadensis (Abrams) Bartel	i	-	-	-	1B.2
	***Hesperocyparis stephensonii* (C. B. Wolf) Bartel**	b	-	-	-	1B.1
Cyperaceae						
	Carex obispoensis Stacey	h	4.9	-	-	1B.2
Ericaceae						
	Arctostaphylos klamathensis S. W. Edwards, Keeler-Wolf & W. Knight	h	3.9	-	-	1B.2
Lamiaceae						
	Acanthomintha ilicifolia A. Gray	o	1.3	CE	FT	1B.1
	Clinopodium chandleri (Brandegee) P.D. Cantino & Wagstaff	h	-	-	-	1B.2
	Lepechinia ganderi Epling	h	-	-	-	1B.3

APPENDIX 1. CONTINUED.

Family	Taxon	Source	Serp.	Rarity CA	FE	CNPS
	Monardella hypoleuca A. Gray subsp. lanata (Abrams) Munz	a	-	-	-	1B.2
	Salvia sonomensis Greene	b	1.6	-	-	-
Liliaceae						
	Calochortus dunnii Purdy	g	-	CR	-	1B.2
	Chlorogalum grandiflorum Hoover	b, l	5.2	-	-	1B.2
Malvaceae						
	***Fremontodendron decumbens* R. M. Lloyd**	e, l	-	CR	FE	1B.2
	Fremontodendron mexicanum Davidson	h	-	CR	FE	1B.1
	Sidalcea elegans Greene	p	-	-	-	3.3
Onagraceae						
	Clarkia delicata (Abrams) A. Nelson & J. F. Macbr.	h	-	-	-	1B.2
	Epilobium minutum Lindl. ex Lehm.	m	2	-	-	-
Orchidaceae						
	Cypripedium californicum A. Gray	p	4.5	-	-	4.2
Orobanchaceae						
	Kopsiopsis hookeri (Walp.) Govaerts	p	-	-	-	2B.3
Picodendraceae						
	Tetracoccus dioicus Parry	a	-	-	-	1B.2
Phrymaceae						
	Mimulus clevelandii Brandegee	h	-	-	-	4.2
Pteridaceae						
	Aspodotis densa (Brack.) Lellinger	k	3.4	-	-	-
Ranunculaceae						
	Delphinium hesperium A. Gray subsp. *cuyamacae* (Abrams) F. H. Lewis & Epling	q	-	CR	-	1B.2
Rhamnaceae						
	Ceanothus ophiochilus S. Boyd, T. S. Ross & Arnseth	h	-	CE	FT	1B.1
	Ceanothus otayensis McMinn	h	-	-	-	1B.2
	***Ceanothus roderickii* W. Knight**	e, g, l	1.7	CR	FE	1B.2
	Frangula californica (Eschsch.) A. Gray subsp. *occidentalis* (Howell ex Greene) Kartesz & Gandhi	c	6	-	-	-
Rosaceae						
	Adenostoma fasciculatum Hook. & Arn.	b	1.3	-	-	-
	Chamaebatia australis (Brandegee) Abrams	h	-	-	-	4.2
	Horkelia truncata Rydb.	h, q	-	-	-	1B.3
Rubiaceae						
	***Galium californicum* Hook. & Arn. subsp. *sierrae* Dempster & Stebbins**	b, l	-	CR	FE	1B.2
Ruscaceae						
	Nolina cismontana Dice	h	-	-	-	1B.2
	Nolina interrata Gentry	e, h	-	CE	-	1B.1
Sarraceniaceae						
	Darlingtonia californica Torr.	p	4.1	-	-	4.2
Themidaceae						
	Brodiaea sierrae R.E. Preston	n	-	-	-	4.3

APPENDIX 2. SPECIES MENTIONED IN THIS APPENDIX DO NOT MEET THE RARITY OR SERPENTINE AFFINITY CRITERIA FOR INCLUSION IN APPENDIX 1, BUT HAVE BEEN NOTED IN THE LITERATURE TO HAVE AN OCCASIONAL AFFINITY FOR GABBRO SOILS IN SOME PART OF THEIR RANGE. Literature sources: a. Baldwin et al. (2012); b. Beauchamp (1986); c. Oberbauer (1993); d. Preston (2006a).

Family	Taxon	Source
Brassicaceae		
	Caulanthus heterophyllus (Nutt.) Payson	b
Hypericaceae		
	Hypericum concinnum Benth.	a
Poaceae		
	Calamagrostis koelerioides Vasey	b
Rhamnaceae		
	Ceanothus foliosus Parry	c
Rosaceae		
	Rubus glaucifolius Kellogg	c
Themidaceae		
	Brodiaea minor (Benth.) S. Watson	d

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EDAPHIC SPECIALIZATION IN THE CRYPTIC SPECIES *MENTZELIA MONOENSIS* (LOASACEAE)

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ABSTRACT

Mentzelia monoensis J. M. Brokaw & L. Hufford is a cryptic hexaploid species known only from Mono County, California. Previous studies have suggested a recent allopolyploid origin of *M. monoensis* but have not investigated the causes of its narrow distribution. Here we report the discovery of a unique haplotype from the chloroplast intergenic spacer *ndhF-rpl32* that is sufficient to distinguish *M. monoensis* from all other species in *Mentzelia* sect. *Trachyphytum* using preserved specimens from any developmental stage. Based on soils collected with verified voucher specimens, we show that the edaphic niche of *M. monoensis* is significantly different from those of all other species in *Mentzelia* sect. *Trachyphytum*. A principal components analysis suggests the edaphic niche of *M. monoensis* is also one of the most extreme in *Mentzelia* sect. *Trachyphytum*. Most populations of *M. monoensis* were collected in soils derived from silica-rich rhyolite tephra produced by the Mono Craters volcanic chain. These coarse textured soils are lower in cation exchange capacity and plant available nutrients than those of any other species in *Trachyphytum*. Our findings suggest that edaphic specialization may have played a significant role in the establishment and geographic distribution of *M. monoensis* and other species in the Mono Basin.

Key Words: Cryptic species, edaphic, endemic, evolution, *Mentzelia*, Mono Craters, polyploidy, rhyolite, specialization.

Mentzelia monoensis J. M. Brokaw & L. Hufford is the most recently described species in *Mentzelia* sect. *Trachyphytum* Torr. & A. Gray, a monophyletic group comprised of roughly 20–30 annual species occurring primarily in western North America (Darlington 1934; Zavortink 1966; Hufford et al. 2003; Brokaw and Hufford 2010a, b, 2011). *Mentzelia* sect. *Trachyphytum* is unique among sections of *Mentzelia* L. for its high number (approximately 2/3 of the named taxa) of polyploid species (Zavortink 1966). *M. monoensis* is hexaploid with a hybrid origin from the progenitors *M. montana* (Davidson) Davidson (tetraploid) and *M. dispersa* S. Watson (diploid or tetraploid) (Brokaw and Hufford 2010b). Most polyploids in *Mentzelia* sect. *Trachyphytum* may be generally characterized as either widespread ruderals or narrowly distributed edaphic specialists (Brokaw 2009). However, *M. monoensis* occurs in both disturbed sites and barren pumice flats in the Long Valley Volcanic Field near Mono Lake, California (Brokaw and Hufford 2011). *Mentzelia monoensis* is thought to be endemic to Mono County (Brokaw and Hufford 2011), and the California Native Plant Society has recently listed *M. monoensis* as a California Rare Plant Rank 4 (plants of limited distribution), which indicates potential for future vulnerability (CNPS 2014). In order to better understand the conservation needs and evolutionary potential of *M. monoensis*, it is necessary to investigate the causes of its narrow distribution.

Considerable attention has been given to the occurrence and causes of rare and endemic species for purposes of both conservation and evolutionary theory (Stebbins 1942; Stebbins and Major 1965; Stebbins 1980; Myers et al. 2000). Although the investigation of endemics is critical to the recognition of general evolutionary trends (Burge and Manos 2011), the distributions of individual species may be determined by unique combinations of historical, genetic, and environmental factors (Stebbins 1980). Historical explanations of endemism have distinguished paleoendemics (relictual endemics that have usually experienced decreases in range size due to environmental change) from neoendemics (recently derived lineages that have never had substantially larger distributions) (Stebbins and Major 1965; Raven and Axelrod 1978). Although the *Mentzelia* sect. *Trachyphytum* crown group is estimated to have diverged 0.8214 (95% CI: 0.09–4.91) million years ago (Schenk and Hufford 2010), it has been suggested that *M. monoensis* and one of its progenitors, *M. montana*, have very recent origins within *Mentzelia* sect. *Trachyphytum* (Brokaw and Hufford 2010b). Thus, as the descendant of a young progenitor, *M. monoensis* is one of the youngest species in a relatively young lineage and is likely best described as a neoendemic both in terms of age and historical distribution. Explanations of limited distribution in neoendemics have included 1) insufficient time for dispersal (Willis 1922), 2) gene pool depletion by genetic drift (Stebbins 1942), and 3) habitat

specialization during speciation (Lewis 1966; Grant 1981). Observations based on the earliest discovered populations of *M. monoensis* have suggested that it is associated with unusual substrates derived from the Mono Craters volcanic chain (Brokaw 2009; Brokaw and Hufford 2011). In this study we focus on characterization of these edaphic conditions in order to test the hypothesis that habitat specialization explains the narrow distribution of *M. monoensis*.

The Long Valley Volcanic Field has experienced abundant volcanic activity for over three million years with some of the most recent eruptions forming the Mono Craters 40,000 to 600 yr ago (Bailey 2004; Riley et al. 2012). Holocene deposits from the Mono Craters are primarily composed of high-silica rhyolite, and these eruptions have left layers of pyroclastic rhyolite to depths of up to two meters throughout the Mono Basin (Bailey 2004; Hildreth 2004; Riley et al. 2012; Bursik et al. 2014). These substrates are potentially stressful habitats for plants because rhyolite weathers more slowly and has lower concentrations of plant-essential elements, including Ca, Fe, and Mg, than igneous rocks with lower silica contents such as basalt (Wolff-Boenisch et al. 2004, 2006; Olsson-Francis et al. 2012). Further, other Mono County endemics, including *Astragalus monoensis* Barneby and *Lupinus duranii* Eastw., are known to be associated with these coarse volcanic soils (Sugden 1985), suggesting edaphic specialization.

Another possible explanation for apparent endemism is our inability to identify *M. monoensis* outside of its known range. This potential deficiency can be attributed to both the short amount of time that *M. monoensis* has existed as a described taxon (Brokaw and Hufford 2011) and the difficulty in distinguishing the species from others in *Mentzelia* sect. *Trachyphytum* (Brokaw and Hufford 2011). Morphologically, *M. monoensis* is difficult to identify because it closely resembles other allopolyploid species in *Mentzelia* sect. *Trachyphytum* with overlapping character states. *Mentzelia monoensis* can usually be identified based on characteristics of seed coats, floral bracts, and leaf color (Brokaw and Hufford 2011). However, identification can be time consuming and inexact, especially among those unfamiliar with *Mentzelia* sect. *Trachyphytum*. Furthermore, these characters are not available in all developmental stages. Consequently, the hexaploid *M. monoensis* cannot always be reliably distinguished from one of its progenitors, the tetraploid *M. montana,* or the closely related octoploid, *M. albicaulis* (Douglas ex Hook.) Douglas ex Torr. & A Gray (Brokaw and Hufford 2010b, 2011).

Due to these difficulties, a practical technique is necessary in order to effectively identify *M. monoensis*. DNA barcoding has significant potential to facilitate plant identification if prospective sequence regions fit the following criteria (Kress et al. 2005). Sequences should be short enough for dependable DNA extraction, amplification, and sequencing, and must exhibit interspecific divergence. However, the ideal sequence should also have intraspecific consistency (Kress et al. 2005). In plants, popular barcoding candidates have included the internal transcribed spacer region (ITS) and the plastid *trnH-psbA* intergenic spacer (Kress et al. 2005). Nevertheless, among closely related species, these markers are not always variable, resulting in the need to investigate other regions. Previous studies in *Mentzelia* sect. *Trachyphytum* have investigated interspecific relationships using five chloroplast intergenic spacers: *trnH-psbA*, *trnS-trnG*, *trnS-trnfM*, *ndhF-rpL32*, and *rpL32-trnL* (Brokaw and Hufford 2010a, b). Therefore, an objective of this study is to test these regions as potential molecular markers to verify identification of *M. monoensis* and its close relatives for the purpose of ecological comparisons.

METHODS

Species Identification

Population sampling. We compared voucher specimens from 70 total populations (Appendix 1), including 24 from *M. monoensis* and 23 from each of the two species most morphologically similar to *M. monoensis*, *M. montana* and *M. albicaulis*. We intensively sampled populations of *M. monoensis* and *M. montana* distributed throughout approximately 1000 km^2 of the Mono Craters volcanic chain in Mono County, California (Fig. 1). We also used specimens from *M. montana* and *M. albicaulis* collected in other parts of Mono County and throughout their ranges in western North America (Fig. 2).

Morphology. Four characters (bract color, bract shape, seed color, and seed coat cell shape) have been previously noted as useful to distinguish *M. monoensis* from *M. montana* and *M. albicaulis* (Brokaw and Hufford 2011). Using the methods of Brokaw and Hufford (2011), we recorded the states from these four morphological characters for all 70 populations in order to compare their consistency with taxon assignments and DNA-based markers. However, in some cases, seed characters had not yet developed on immature vouchers.

DNA isolation and analysis. All cpDNA sequences generated in this study have been deposited with NCBI GenBank (see Appendix 1). DNA extraction was performed for 11 of the vouchers of *M. monoensis M. montana*, and *M. albicaulis* in a previous study by Brokaw and

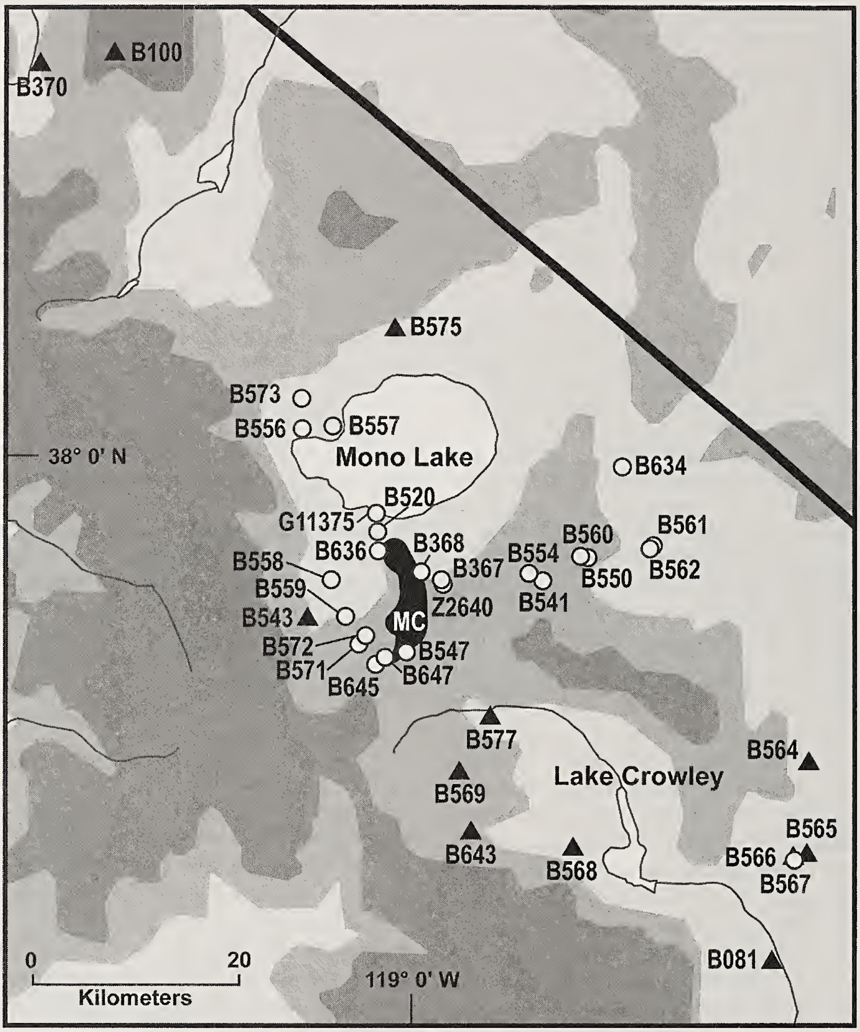

FIG. 1. Sampling map for the Mono Basin region, Mono County, California. Soil and/or genetic sampling locations indicated by open circles (*M. monoensis*) or closed triangles (*M. montana*). MC: location of the Mono Craters indicated in black. Shaded relief layers represent elevations less than 3000 m (light grey), 3000 to 4000 m (medium grey), and greater than 4000 m (dark grey). Sample labels represent abbreviated voucher collection numbers (see Appendix 1).

Hufford (2010b). Total genomic DNA from the 59 new populations was isolated from 10 mg of silica-gel-dried or herbarium specimen leaf material. The plant tissues were ground to a fine powder, and genomic DNA extraction was carried out with an EZNA Plant DNA Kit (Omega Bio-Tek, Norcross, GA) following the manufacturer's instructions. The chloroplast spacers *trnH-psbA* and *ndhF-rpL32* were amplified using PCR as described in Marlowe and Hufford (2007). PCR products were sequenced directly.

The PCR protocol for plastid spacers consisted of a 25 μL sample containing 13.8 μL H_2O, 2.5 μL 10× Thermopol Reaction Buffer with 20 mM Mg^{2+} (New England Biolabs, Ipswich, MA), 2.5 μL of each 5 μM primer, 1.5 μL 2.5 mM dNTP, 0.2 μL 5 U/μL Taq polymerase (New England Biolabs), and 2.0 μL diluted DNA template of unknown concentration. PCR conditions in a Biometra thermocycler (Whatman, Göttingen, Germany) included initial denaturation at 94°C for 5 min; followed by 30 cycles at 94°C for 1 min, 55°C for 1 min, and 72°C for 2 min; with a final extension at 72°C for 7 min.

All PCR products were visualized by 1% agarose gel electrophoresis and purified with an EZNA Cycle-Pure Kit (Omega Bio-Tek, Norcross, GA) following the manufacturer's instructions, and the purified product was sequenced at the DNA Analysis Facility at Yale University. Sequences were assembled and edited using the program Sequencher version 5.2.4 (Gene Codes Corp., Ann Arbor, MI). New *trnH-psbA* and

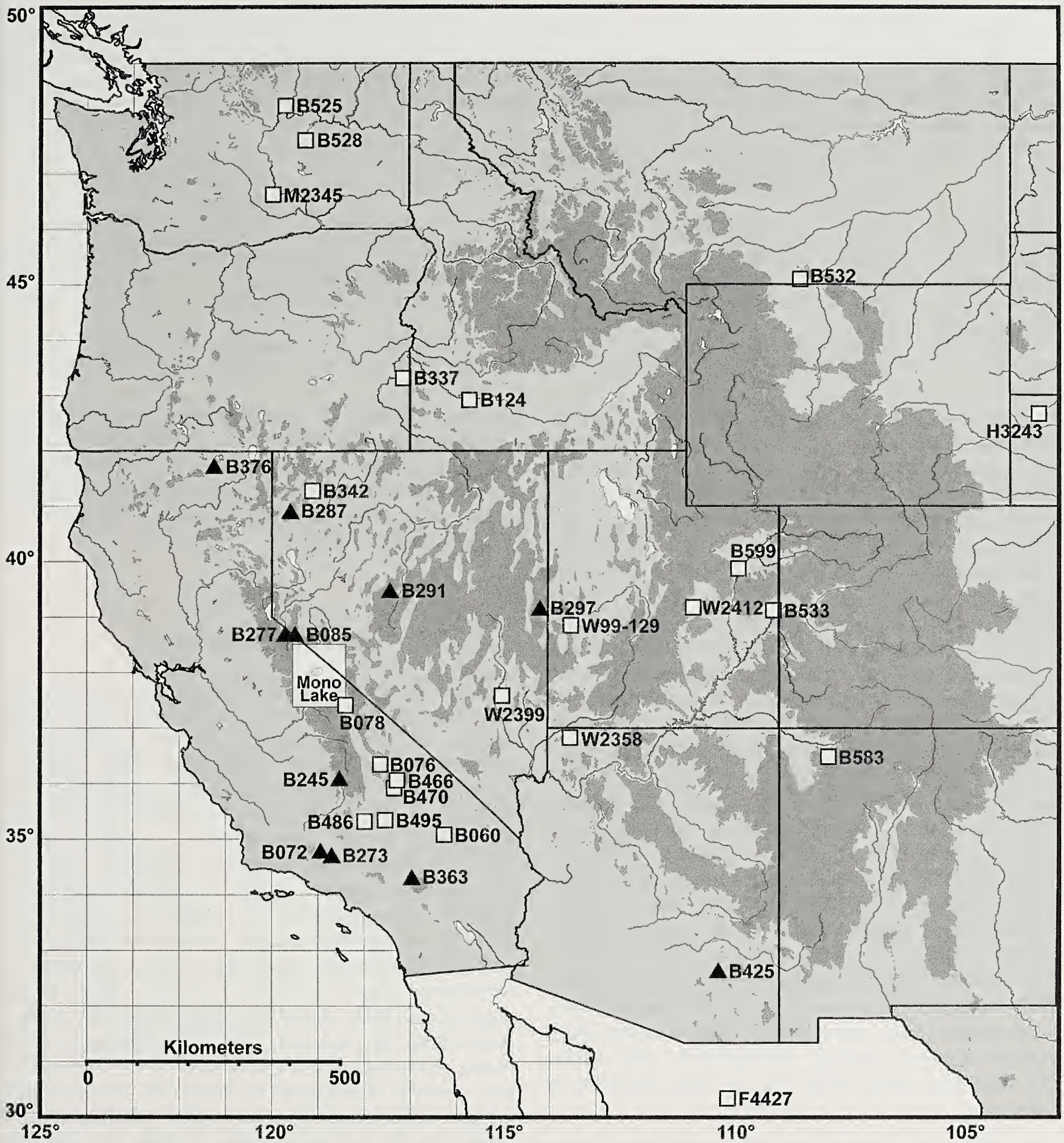

FIG. 2. Sampling map for western North America. Soil and/or genetic sampling locations indicated by closed triangles (*M. montana*) or open squares (*M. albicaulis*). White rectangle encompassing Mono Lake indicates the distribution of *M. monoensis* shown in Fig. 1. Shaded relief layers represent elevations less than 2000 m (light grey) and greater than 2000 m (dark grey). Sample labels represent abbreviated voucher collection numbers (see Appendix 1).

ndhF-rpL32 sequences and those for all five chloroplast intergenic spacers (*trnH-psbA, trnS-trnG, trnS-trnfM, ndhF-rpL32, rpL32-trnL*) from the 11 vouchers of *M. monoensis M. montana*, and *M. albicaulis* previously sequenced by Brokaw and Hufford (2010b) were combined for analysis. Sequences were aligned manually using SE-AL (v2.0a11; Rambaut 1996–2002). Haplotype networks were constructed using TCS version 1.21 (Clement et al. 2000) under the criterion of a parsimony network in which connections have a probability of at least 95%.

Edaphic Characterization

Edaphic data. In 2013, we collected soils from 17 locations within the range of *M. monoensis* representing 15 populations of *M. monoensis*, one population of *M. montana*, and one mixed population of *M. monoensis* and *M. montana*

TABLE 1. INTRASPECIFIC CHARACTER STATE CONSISTENCY OF BRACT COLOR, BRACT SHAPE, SEED COLOR, AND SEED COAT CELL SHAPE IN *M. ALBICAULIS*, *M. MONOENSIS*, AND *M. MONTANA*. For each character, the most common (dominant) of two possible character states and the percentage of specimens exhibiting the dominant state are listed. For bract shape, the less common character state for all species was toothed/lobed. The number of specimens of each species with observable character states is provided; seed color was not reported for seeds darkened during preservation.

	M. albicaulis		*M. monoensis*		*M. montana*	
Character	Dominant state	% consistent	Dominant state	% consistent	Dominant state	% consistent
Bract color	Green	100.00 (n = 23)	Green	69.57 (n = 24)	White base	82.61 (n = 23)
Bract shape	Entire	52.17 (n = 23)	Entire	100.00 (n = 24)	Entire	52.17 (n = 23)
Seed color	Tan	60.00 (n = 10)	Tan	100.00 (n = 21)	Spotted	82.35 (n = 17)
Seed coat cell shape	Pointed	100.00 (n = 15)	Domed	100.00 (n = 22)	Pointed	100.00 (n = 21)

(Appendix 2). In order to compare the edaphic habitats of *M. monoensis* to those of other taxa, we combined this new data with previously collected soils data (Brokaw 2009) from 226 locations representing the distributional and ecological ranges of each of the 24 North American species in *Mentzelia* sect. *Trachyphytum* that have been recognized by Zavortink (1966), Thompson and Roberts (1971), Glad (1976), and Brokaw and Hufford (2010b). The combined data set included samples from 19 populations of *M. monoensis*, 32 populations of *M. montana,* and 32 populations of *M. albicaulis.* Soils were collected as composite samples composed of five 0–15 cm depth soil cores for each locality and sieved to remove particles greater than two mm. Soil diagnostic services were provided by MDS Harris Laboratories (Lincoln, NE). Edaphic data used for comparisons consisted of percent composition of sand, silt, and clay particle sizes, percent soil organic matter (SOM), cation exchange capacity (CEC), pH, concentration of soluble salts (salinity), boron (B), calcium (Ca), copper (Cu), iron (Fe), potassium (K), magnesium (Mg), manganese (Mn), sodium (Na), nitrate-nitrogen (NO_3), phosphorus (P), sulfur (S), and zinc (Zn), from the <2 mm fraction of substrate.

Statistical analyses. Differences in species habitats based on the selected edaphic variables were visualized in multidimensional space using principal components analysis (PCA) of the 243 population soil samples with the CANOCO for Windows software package 4.5.1 (ter Braak and Šmilauer 2002; Lepš and Šmilauer 2003). To test for significant differences between species edaphic niches as represented by groups of population soil samples, an NPMANOVA (Anderson 2001) was conducted using the Euclidean distance matrices created from pair-wise comparisons of population habitat samples. NPMANOVA is a method for multivariate analysis of variance based on Monte-Carlo permutations, that tests for differences in locations of centroids among groups of observations based on the chosen distance measure. NPMANOVA was performed with 9999 unrestricted permutations of the raw data (after centering and standardization) using the software package PAST 2.17 (Hammer et al. 2001).

RESULTS

Species Identification

Morphology. Seed coat cell shape was the only morphological character with uniform states within all three species (Table 1). *Mentzelia monoensis* has domed seed coat cells, and *M. montana* and *M. albicaulis* have pointed seed coat cells (see Brokaw and Hufford 2011). All specimens of *M. monoensis* had entire bracts and tan seeds, but both *M. montana* and *M. albicaulis* are polymorphic for these characters, and *M. monoensis* is polymorphic for bract color. Only 57 of the 70 voucher specimens (81%) had sufficiently mature seeds that could be used to determine seed coat cell shape, and bract characters alone could not distinguish *M. monoensis* from *M. montana* and *M. albicaulis* in all cases. Although fresh specimens of *M. monoensis* can usually distinguished from *M. montana* by subtle differences in leaf color (Brokaw and Hufford 2011), this character was not reliable for preserved specimens and our final determinations of species identities were not based on morphology if seed coat cell shape could not be determined.

DNA isolation and analysis. The *ndhF-rpL32* intergenic spacer was determined to be the most useful genetic marker for identification of *M. monoensis.* Preliminary analyses of three of the five chloroplast spacers (*trnS-trnG*, *trnS-trnfM*, *rpL32-trnL*) revealed that *M. monoensis* lacked unique variation in these regions that could be used for discrimination from *M. montana* and *M. albicaulis*; no further sequencing was performed using these markers. Some populations of *M. monoensis* (B367, B547, Z2640) were found to

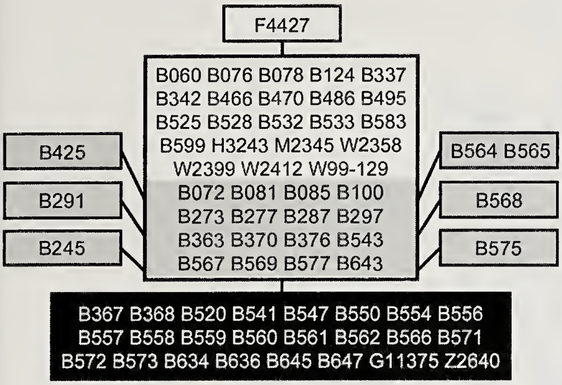

FIG. 3. Haplotype network of *ndhF-rpL32* sequences generated in TCS. Rectangles correspond to sampled haplotypes from *M. monoensis* (black), *M. montana* (grey), and *M. albicaulis* (white). Lines connecting haplotypes represent a single substitution. Sample labels represent abbreviated voucher collection numbers (see Appendix 1).

contain a unique nucleotide substitution in *trnH-psbA*. However, subsequent sampling determined that this haplotype was limited to populations near the type locality of *M. monoensis* (including collections from as early as 1966 and as recently as 2009) but not present in most populations of *M. monoensis*. Therefore, because many populations of *M. monoensis* have the same *trnH-psb A* haplotype as *M. montana* and *M. albicaulis*, sequencing of *trnH-psbA* was also discontinued. The most common haplotype of *ndhF-rpL32* was shared by most specimens of *M. montana* and *M. albicaulis*; six haplotypes in *M. montana* and one additional haplotype in *M. albicaulis* each differed from the most common haplotype by a single substitution (Fig. 3). None of the haplotypes from *M. montana* and *M. albicaulis* were shared by *M. monoensis*. All specimens of *M. monoensis* had an identical *ndhF-rpL32* haplotype that was unique to *M. monoensis* and differed from the most common haplotype in and *M. albicaulis* by a single nucleotide substitution of a C-G pair (present in *M. monoensis*) for an A-T pair (present in *M. montana* and *M. albicaulis*). This transversion in *ndhF-rpL32* also distinguishes *M. monoensis* from all other species in *Mentzelia* sect. *Trachyphytum* analyzed by Brokaw and Hufford (2010b). Further, among vouchers in this study that had mature seeds, this single nucleotide polymorphism (SNP) showed a perfect correlation with seed coat cell shape. Thus this C-G/A-T SNP has become the most reliable character currently available for identification of herbarium specimens of *M. monoensis* at all stages of development. Therefore, specimens in this study lacking mature seeds were identified using this marker if chromosome counts were not available.

Edaphic Characterization

Principal components analysis suggests that the edaphic niche of *M. monoensis* is extreme with respect to those of other species, including the progenitors of *M. monoensis* (Fig. 4). The first two principal components account for 52.6% of total variance, with 32.3% on the first principal component and 20.3% on the second. The first principal component (PC1) is positively correlated with percent sand (vector loading = 0.71) and strongly negatively correlated with cation exchange capacity (vector loading = 0.94) and concentration of soluble salts (vector loading = 0.91). The second principal component (PC2) is positively correlated with extractable phosphorus (vector loading = 0.79), zinc (vector loading = 0.76), manganese (vector loading = 0.74), and iron (vector loading = 0.73) and soil organic matter (vector loading = 0.72) and negatively correlated with pH (vector loading = 0.70). These results are summarized in a biplot of the first two principal components (Fig. 4). In the biplot of PC1 and PC2 only five populations of other species including one from *M. montana* and two from *M. albicaulis* are positioned within the two dimensional envelope representing all 19 sampled populations from *M. monoensis*. Populations from *M. monoensis* represented the seven highest sample values on PC1. The three samples with highest overall values on PC1 (B647, B572, B547) were also among those collected nearest the Mono Craters chain (Fig. 1); a fourth of these nearest samples (B636) was collected from a recently burned site and had the lowest PC1 value of any *M. monoensis* soil. Three of the six *M. monoensis* samples with lowest PC1 scores (B573, B556, B557) were collected on or nearest Black Point, a basaltic cinder cone on the northwestern shore of Mono Lake, and the remaining two lowest (B645 and B562) were collected along the disturbed margins of paved highways near the southwestern and northeastern edges of the *M. monoensis* range respectively (Fig. 1). The southeastern most sampled population of *M. monoensis* (B566) was nearly 30 km from the nearest known population of *M. monoensis* and had an intermediate PC1 value with respect to other *M. monoensis* samples. At this disjunct location, *M. monoensis* was found growing in a mixed population with *M. montana* (B567), representing the highest PC1 sample value for *M. montana* in this study. In contrast to PC1, populations from *M. monoensis* did not have extreme values on PC2. Values from *M. monoensis* samples fell completely within and spanned most of the range of values for other species in *Mentzelia* sect. *Trachyphytum*, although the burned B636 site was a high outlier on PC2 compared to other *M. monoensis* samples. Differences between sets of soil samples grouped by species were tested with

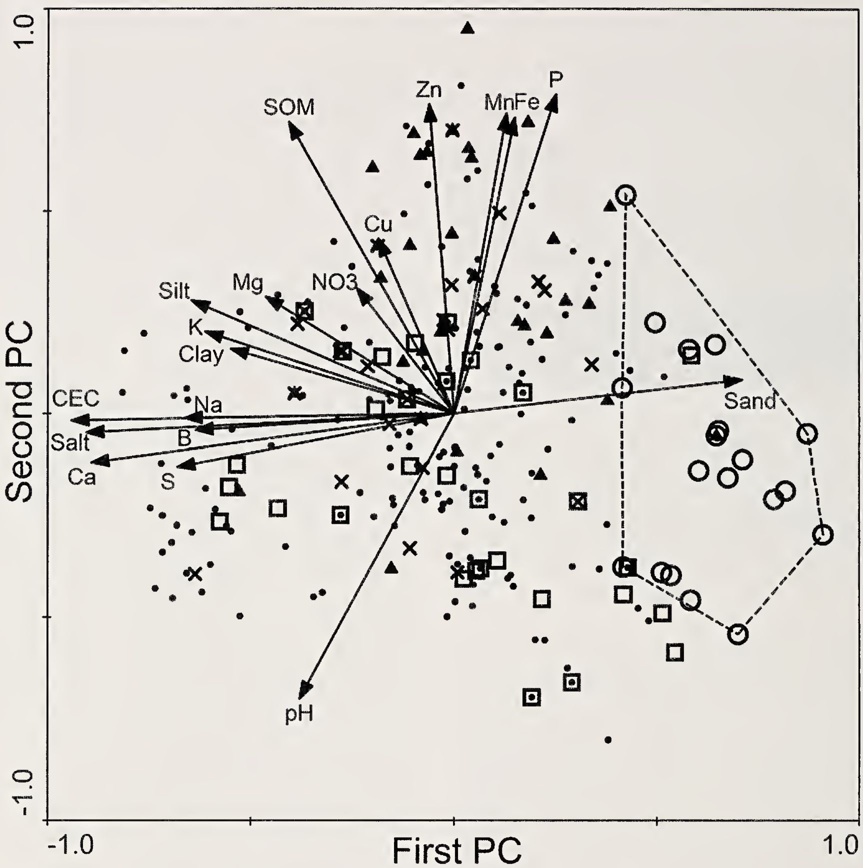

FIG. 4. Biplot for the first two principal components from principal components analysis (PCA) of soil chemistry and texture data for 243 assayed soil samples; the first PC represents 32.3% of total variance; the second PC represents 20.3% of total variance; arrows represent direction and magnitude of loading for soil variables on the principal component axes; open circles and dashed envelope represent soils from *M. monoensis*; closed triangles represent *M. montana*; open squares represent *M. albicaulis*; X-marks represent *M. dispersa*; points represent all other North American species in *Mentzelia* sect. *Trachyphytum*. Symbols: CEC = cation exchange capacity; N03 = nitrate; SOM = soil organic matter.

NPMANOVA. The NPMANOVA showed that the sampled soils of *M. monoensis* were significantly different ($P < 0.0001$) from those of all other North American species in *Mentzelia* sect. *Trachyphytum*, including *M. montana* and *M. albicaulis*.

Discussion

Mentzelia monoensis is a unique species that can be reliably distinguished from its closest relatives with a simple genetic marker. The distinct hexaploid karyotype of *M. monoensis* has been recognized for over 50 yr (Zavortink 1966). However, its morphology, geography, and evolution had not been thoroughly investigated until recently due in part to the lack of reliable morphological characters for identification (Brokaw and Hufford 2010b, 2011). In addition to broadening our understanding of the morphological and geographic variation in *M. monoensis*, recent work has suggested a unique origin story; *M. monoensis* is the only allopolyploid thought to have formed through a hybridization involving the two major subclades within *Mentzelia* sect. *Trachyphytum*, "Affines" and "Trachyphyta," via the progenitors *M. dispersa* (diploid or tetraploid) and *M. montana* (tetraploid) respectively (Brokaw and Hufford 2010b). With the discovery of unique variation in the *ndhF-rpL32* intergenic spacer for use as a genetic barcode for *M. monoensis*, the reliability of identification is now sufficient to support ecological and biogeographic investigations based on fresh and preserved voucher specimens at all developmental stages. Although *ndhF-rpL32* has not proven to be sufficiently variable to provide unique haplotypes for some species, including *M. montana* and *M. albicaulis*, the simplicity of the unique character (a single nucleotide transversion) distinguishing *M. monoensis* from other species will allow for more rapid and cost effective identifi-

cation of candidate specimens through the development of allele specific PCR protocols (Gaudet et al. 2007, 2009). The need to use molecular technologies for reliable identification can be a burdensome addition to ecological investigations, but reliance on morphology-based taxonomy has resulted in the underrepresentation of species richness in nature and obscured insight into ecology and evolution (Soltis et al. 2007). Prior to the availability of molecular and cytological evidence this bias has concealed the unique ecological status of *M. monoensis* revealed by this study.

Now with a reliable method for identification, we suggest that the apparent endemism of *M. monoensis* is most likely the result of edaphic specialization for the volcanic substrates of the Mono Basin rather than simply a byproduct of misidentification. An NPMANOVA based on measured soil characteristics suggests that the edaphic niche of *M. monoensis* is significantly different from those of all other species in *Mentzelia* sect. *Trachyphytum*. According to principal components analysis of these data (Fig. 4), the edaphic niche of *M. monoensis* is also one of the most extreme in *Mentzelia* sect. *Trachyphytum*. *Mentzelia monoensis* is found in soils that are generally coarser in texture and lower in cation exchange capacity and plant available nutrients than those of other species in its section. These findings are consistent with the chemical content and weathering rates of silica-rich rhyolites deposited in the Mono Basin during the most recent eruptions of the Mono Craters (Patten et al. 1987; Bailey 2004; Wolff-Boenisch 2004, 2006). In agreement with an edaphic explanation for the distribution of *M. monoensis*, the tephra fields of the Long Valley Volcanic Chain differ substantially in chemical composition from soils from comparable elevation and vegetation types in the Great Basin (Patten et al. 1987), and *M. monoensis* is primarily limited to soils derived from these deposits. Although experimental data on *M. monoensis* and related species grown under reciprocal conditions could yield more conclusive insights about the role of edaphic specialization in geographic isolation, the hypothesis of edaphic constraints is consistent with observed physical and chemical gradients in the Mono Craters tephras. For example, the soil samples from *M. monoensis* in this study with the most extreme values with respect to other species in *Mentzelia* sect. *Trachyphytum* are closest to the Mono Craters, and those with the least extreme values are near the edges of the *M. monoensis* distribution. The positions of these gradients are explained by the observation that eruptions deposit the deepest, coarsest tephra nearest the Mono Craters (Bailey 2004).

As a putative Mono County endemic, *M. monoensis* has a unique geographic distribution in *Mentzelia* sect. *Trachyphytum*. Most species in *Mentzelia* sect. *Trachyphytum* have at least a portion of their distributions in southern California, suggesting that southern California is either an ancestral or refugial region for *Mentzelia* sect. *Trachyphytum* as a whole (Brokaw et al. 2011). Of the few examples of species distributed entirely outside of southern California, all are species that have been associated with unusual soil conditions: *M. crocea* Kellogg and *M. lindleyi* Torr & A. Gray with serpentine soils (Zavortink 1966), *M. mollis* M. Peck and *M. packardiae* J. B. Glad with saline-sodic soils (Glad 1976), *M. thompsonii* J. B. Glad with calcareous soils (Brokaw et al. 2011), and *M. monoensis* with nutrient deficient soils (Brokaw and Hufford 2011). Although explanations of endemism likely involve a combination of historical, genetic, and environmental factors (Stebbins 1980), this pattern suggests that adaptation to localized edaphic conditions has played a major role in the distributions of these disjunct endemics. Further, the narrow distributions of other endemic plant species in the Mono Basin tephra fields (Sugden 1985) provide support for the role of the Mono Craters in the repeated creation of edaphic endemics, including *M. monoensis*.

Edaphic factors have long been regarded as potential drivers of plant diversification (Stebbins 1942; Kruckeberg 1986; Rajakaruna 2004). Because *M. monoensis* is a relatively young neoendemic, it is likely that the edaphic specialization associated with its narrow distribution resulted from and promoted its establishment as a new species. Although polyploidization has often been considered a form of instant, sympatric speciation in the context of biological species concepts (Coyne and Orr 2004), the subsequent establishment of a self-sustaining polyploid population can be threatened by reproductive competition from sympatric progenitors (Hagberg and Ellerstrom 1959; Levin 1975). Factors that may alleviate this minority cytotype disadvantage include self-pollination (Levin 1975), stochastic effects (Rausch and Morgan 2005), and adaptive/ecological advantages (Leitch and Leitch 2008, Ramsey 2011). *Mentzelia monoensis*, like other species in *Mentzelia* sect. *Trachyphytum*, is capable of substantial self-fertilization (Zavortink 1966). However, predominant selfing alone cannot explain successful establishment in the absence of chance events and/or ecological divergence (Levin 1975, Felber 1991). Adaptation has been used to explain the successful establishment of new cytotypes either following stochastic events (Lewis 1961, 1966) or as a result of novel traits caused by the polyploidization itself (Ramsey 2011). A critical factor in both explanations is that spatial isolation of new polyploids from the source populations is required and must be maintained until the polyploid population is

capable of eliminating or coexisting with migrants with other cytotypes (Lewis 1961, 1966). Based on these premises, the simplest explanation for the establishment of *M. monoensis* is that the new hexaploid population(s) multiplied in isolation from diploid and tetraploid progenitors and relatives after stochastic dispersal event(s) fortuitously placed the first hexaploid seed(s) in the uncolonized ejecta from the recently formed Mono Craters. This scenario does not require that progenitor species be incapable of colonizing the same habitats. Most species in *Mentzelia* sect. *Trachyphytum* exhibit spotty, stochastic colonization patterns of populations interspersed among many suitable but unused habitats (personal observation). This suggests that the lucky placement of a new polyploid seed in an uninhabited location may be the first and most critical step in establishment. According to this hypothesis, the eruptions of the Mono Craters may have been more important as mechanisms for providing new cleared space for colonization than for the chemical characteristics of their deposits. However, following successful dispersal and population establishment, it has been suggested that polyploidization may confer novel traits and/or more rapid responses to natural selection in ways that facilitate specialization for the new habitats (Leitch and Leitch 2008, Ramsey 2011). Once establishment is secured, an additional adaptive advantage to the neopolyploid is the postzygotic suppression of gene flow that might otherwise impede ecological divergence from progenitors and specialization to new substrates (Lewis 1962, 1966). In agreement with this assertion of suppressed gene flow, controlled crosses between *M. monoensis* and other species in *Mentzelia* sect. *Trachyphytum* have revealed strong reproductive isolation (Zavortink 1966). In crosses with hexaploids, *M. monoensis* either produced a small number of nonviable seeds or failed to produce seeds entirely, and all crosses in *Mentzelia* sect. *Trachyphytum* involving mixed ploidy levels resulted in 99–100% reduction in seed production and no germination (Zavortink 1966). Together these genetic and biogeographic circumstances might provide neopolyploids with an evolutionary trajectory very different from that of the parental species (Lewis 1966). Thus, morphologically cryptic differences in karyotype could have important ecological consequences (Soltis et al. 2007).

Although escape from endemism caused by edaphic specialization has been inferred to be rare (Anacker 2011), it might be premature to conclude that *M. monoensis* is an "evolutionary dead-end" (Anacker 2011, p. 374). Ongoing adaptive potential has been inferred for both habitat specialists and polyploid species (Nosil and Mooers 2005; Otto 2007). Stebbins (1942) first proposed that neoendemics become constrained to a narrow distribution through loss of genetic variation by genetic drift and/or natural selection, and this expectation of genetic depletion in *M. monoensis* is supported by sequence data from *ndhF-rpL32* that suggests *M. monoensis* has lower cpDNA diversity than *M. montana* and *M. albicaulis*. However, these data do not take into account the diversifying effects of allopolyploidization on the nuclear genome of *M. monoensis* (Otto 2007; Leitch and Leitch 2008). Further support for the potential of *M. monoensis* to acquire a different or more generalized niche may be gained from the observation that many of the *M. monoensis* habitats with the least extreme chemical characteristics had been subjected to burning or mechanical disturbance. This suggests that *M. monoensis* is capable of inhabiting a wider variety of soil conditions when competition is reduced through disturbance. Other edaphic endemics in *Mentzelia* sect. *Trachyphytum*, including *M. mollis* and *M. packardiae*, have similar patterns of distribution on stressful and disturbed soils and have even been successfully grown in standard potting soil (Brokaw, personal observation), suggesting that these unusual substrates may act as a refuge from competition rather than providing essential chemical resources. Finally, *M. monoensis* has been found in mixed populations with both *M. montana* and the diploid *M. congesta* Torr. & A. Gray (Brokaw, personal observation), suggesting that at least temporary coexistence is possible with other species in *Mentzelia* sect. *Trachyphytum*, albeit usually at the edges of the *M. monoensis* range.

It is also possible that further range expansion will be achieved by *M. monoensis* without any significant adaptive change. Although the historical explanation that neoendemics are narrowly distributed simply because they have had insufficient time for dispersal (Willis 1922) has been thoroughly criticized (Stebbins 1980), species age may play a major role in the likelihood of improbable events such as long distance dispersal to islands of habitat suitable for edaphic specialists (MacArthur and Wilson 1967). Although still within the boundaries of Mono County, one population of *M. monoensis* (B566) has already been found nearly 30 km southeast of the next closest population. No other known populations of *M. monoensis* are separated from their nearest neighbors by more than 10 km. However, the soil properties from this disjunct location do not suggest a new or marginal habitat. Rather, the B566 site is still part of the same Long Valley Volcanic Field that contains Mono Craters (Bailey 2004), and the chemical and physical properties from this site fell near the middle of the distribution of properties from soils collected within the contiguous *M. monoensis* range. *Mentzelia monoensis* has not been found in the

intervening region separating the B566 site from the contiguous *M. monoensis* range because the Glass Mountain Ridge is higher in elevation and lacks the deep ash deposits found both at B566 and surrounding the Mono Craters (Bailey 2004). For the same reasons, *M. monoensis* has also not been found on the steep peaks in the heart of the Mono Craters chain. The occurrence of the B566 population suggests that *M. monoensis* can colonize disjunct habitats if the soils are suitable, but substantial time might be necessary for additional range expansions through low frequency dispersals when suitable sites (if they exist) occur at great distances.

Nevertheless, the future of any neopolyploid is precarious due to its initially narrow distribution (Leitch and Leitch 2008), and the fate of *M. monoensis* remains unclear. We have not identified any imminent threats to the persistence of *M. monoensis*, and, where it is found, *M. monoensis* is often abundant and tolerates or responds favorably to intermediate levels of disturbance associated with road maintenance, hillside erosion, and fire (Brokaw, personal observation). However, *M. monoensis* is an annual species that presumably requires favorable conditions for germination and growth that are vulnerable to climate change. Interestingly, some edaphic endemics in *Mentzelia* sect. *Trachyphytum*, including *M. mollis* and *M. thompsonii*, appear to be paleoendemics with disjunct distributions caused by their successful persistence on unusual substrates in the face of shifting conditions during episodes of prehistoric climate change (Glad 1975; Brokaw et al. 2011). However, adaptation models suggest that extinction rather than evolution is likely if environmental conditions change too rapidly (Hoffman and Sgró 2011).

The Mono Lake region has been an area of concern for conservationists as a result of unnatural diversion of water pathways and the resulting changes in aquatic ecology that have been further exacerbated by human induced climate change (Patten et al. 1987; Wiens et al. 1993; Millar and Woolfenden 1999). However, the same geological forces that created Mono Lake have also generated a unique edaphic environment throughout the semi-arid terrestrial communities of the Mono Basin (Patten et al. 1987; Bailey 2004). Although a small number of plants endemic to the Mono Basin have been discovered (Sugden 1985), it is possible that other undiscovered endemics are present. Finally, it must be acknowledged that we cannot be fully confident that we have identified the entire geographic range circumscribing the putative endemism of *M. monoensis*. However, we expect that any major range extensions would represent narrow disjunct distributions likely associated with similar edaphic conditions. Regardless of any such discoveries, observations from this study confirm that *M. monoensis* is a unique, albeit cryptic, component of the remarkable Mono Basin ecosystem.

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APPENDIX 1

Voucher information and GenBank accessions for specimens in this study. Missing data are indicated with an en dash (–). **Voucher code:** Voucher *collector* and *collection number*, deposition herbarium acronym, latitude, longitude, elevation in meters; GenBank accession numbers for *ndhF-rpL32*, *trnH-psbA*. ACU: Abilene Christian University Herbarium; LA: University of California, Los Angeles Herbarium; UT: Utah Museum of Natural History, Garrett Herbarium; WS: Marion Ownbey Herbarium.

Mentzelia albicaulis

B060: *Brokaw 060* (WS), 35.06260, −116.28833, 356 m; KM043532, –. **B076:** *Brokaw 076* (WS), 36.30335, −117.63695, 1631 m; KM043533, –. **B078:** *Brokaw 078* (WS), 37.15513, −118.28947, 1236 m; KM043534, –. **B124:** *Brokaw 124* (WS), 42.90667, −115.69203, 762 m; KM043535, –. **B337:** *Brokaw 337* (WS), 43.28265, −117.25745, 1177 m; FJ917857, FJ918127. **B342:** *Brokaw 342* (WS), 41.22359, −119.07072, 1391 m; KM043536, –. **B466:** *Brokaw 466* (WS), 35.98656, −117.34270, 661 m; KM043537, –. **B470:** *Brokaw 470* (WS), 35.89770, −117.33201, 704 m; KM043538, –. **B486:** *Brokaw 486* (WS), 35.31596, −118.05270, 758 m; KM043539, –. **B495:** *Brokaw 495* (WS), 35.36298, −117.63688, 1185 m; KM043540, –. **B525:** *Brokaw 525* (WS), 48.21440, −119.70982, 270 m; KM043541, –. **B528:** *Brokaw 528* (WS), 47.62568, −119.34213, 522 m; KM043542, –. **B532:** *Brokaw 532* (WS), 45.05924, −108.66726, 1381 m; KM043543, –. **B533:** *Brokaw 533* (WS), 39.03924, −109.28689, 1382 m; KM043544, –. **B583:** *Brokaw 583* (ACU), 36.53905, −107.95961, 1938 m; KM043545, –. **B599:** *Brokaw 599* (ACU), 39.94981, −109.90137, 1563 m; KM043546, –. **F4427:** *Fishbein 4427* (WS), 30.36, −110.60, 950 m; FJ917858, FJ918128. **H3243:** *Hufford 3243* (WS), 42.58, −103.40, 1350 m; FJ917859, FJ918129. **M2345:** *Mastrogiuseppe 2345* (WS), 46.91, −119.98, 150 m; FJ917860, FJ918130. **W2358:** *Windham 2358* (UT), 36.83083, −113.573056, 1487 m; KM043547, –. **W2399:** *Windham 2399* (UT), 37.59788, −115.054263, 1471 m; KM043548, –. **W2412:** *Windham 2412* (UT), 39.20328, −110.86160, 1738 m; KM043549, –. **W99−129:** *Windham 99–129* (UT), 38.83605, −113.515268, 1769 m; KM043550, –.

Mentzelia monoensis

B367: *Brokaw 367* (WS), 37.89570, −118.97472, 2257 m; FJ917907, FJ918178. **B368:** *Brokaw 368* (WS), 37.90589, −118.98978, 2118 m; KM043492, KM043552. **B520:** *Brokaw 520* (WS), 37.92793, −119.04869, 2118 m; FJ917908, FJ918179. **B541:** *Brokaw 541* (ACU), 37.89570, −118.97472, 2257 m; KM043493, –. **B547:** *Brokaw 547* (ACU), 37.82022, −119.00142, 2354 m; KM043494, KM043551. **B550:** *Brokaw 550* (ACU), 37.89451, −118.85307, 2456 m; KM043495, –. **B554:** *Brokaw 554* (ACU), 37.89023, −118.86738, 2481 m; KM043496, KM043553. **B556:** *Brokaw 556* (ACU), 38.02101, −119.13085, 1975 m; KM043497, KM043554. **B557:** *Brokaw 557* (ACU), 38.02763, −119.08554, 1972 m; KM043498, KM043555. **B558:** *Brokaw 558* (ACU), 37.88666, −119.09028, 2103 m; KM043499, KM043556. **B559:** *Brokaw 559* (ACU), 37.86439, −119.08492, 2161 m; KM043500, KM043557. **B560:** *Brokaw 560* (ACU), 37.89059, −118.78930, 2243 m; KM043501, KM043558. **B561:** *Brokaw 561* (ACU), 37.92131, −118.70541, 2008 m; KM043502, KM043559. **B562:** *Brokaw 562* (ACU), 37.91792, −118.71134, 2048 m; KM043503, KM043560. **B566:** *Brokaw 566* (ACU), 37.63795, −118.63873, 2247 m; KM043504, KM043561. **B571:** *Brokaw 571* (ACU), 37.84638, −119.06704, 2236 m; KM043505, KM043562. **B572:** *Brokaw 572* (ACU), 37.84789, −119.06490, 2225 m; KM043506, KM043563. **B573:** *Brokaw 573* (ACU), 38.05379, −119.12708, 2054 m; KM043507, KM043564. **B634:** *Brokaw 634* (ACU), 37.98300, −118.73704, 2101 m; KM043508, –. **B636:** Brokaw 636 (ACU), 37.91346, −119.04558, 209 m; KM043509, –. **B645:** *Brokaw 645* (ACU), 37.80689, −119.04564, 2391 m; KM043510, –. **B647:** *Brokaw 647* (ACU), 37.81412, −119.03428, 2350 m; KM043511, –. **G11375:** *Grable 11375* (WS), 37.94, −119.05, 1950 m; KM043512, –. **Z2640:** *Zavortink 2640* (LA), 37.89570, −118.97472, 2250 m; FJ917909, FJ918180.

Mentzelia montana

B081: *Brokaw 081* (WS), 37.50808, −118.58355, 1770 m; KM043514, KM043566. **B085:** *Brokaw 085* (WS), 38.64287, −119.54777, 1605 m; FJ917910, FJ918181. **B100:** *Brokaw 100* (WS), 38.34870, −119.36365, 2290 m; KM043515, KM043567. **B245:** *Brokaw 245* (WS), 35.97818, −118.54830, 1544 m; KM043526, KM043568. **B273:** *Brokaw 273* (WS), 34.77523, −118.97, 2436 m; KM043516, KM043569. **B277:** *Brokaw 277* (WS), 38.67768, −119.73907, 1730 m; FJ917930, FJ918201. **B287:** *Brokaw 287* (WS), 40.88940, −119.61382, 1762 m; KM043517, KM043570. **B291:** *Brokaw 291* (WS), 39.23950, −117.77805, 1902 m; KM043527, KM043571. **B297:** *Brokaw 297* (WS), 39.02630, −114.25310, 2463 m; KM043518, –. **B363:** *Brokaw 363* (WS), 34.26765, −116.94305, 2071 m; KM043519, –. **B370:** *Brokaw 370* (WS), 38.34375, −119.43793, 2193 m; FJ917931, FJ918202. **B376:** *Brokaw 376* (WS), 41.66470, −121.25054, 1274 m; KM043520, –. **B425:** *Brokaw 425*

(WS), 32.53211, −110.71064, 1484 m; FJ917911, FJ918182. **B543:** *Brokaw 543* (ACU), 37.85869, −119.12144, 2274 m; KM043521, KM043572. **B564:** *Brokaw 564* (ACU), 37.72669, −118.59816, 2210 m; KM043528, KM043573. **B565:** *Brokaw 565* (ACU), 37.65005, −118.61573, 2232 m; KM043529, KM043574. **B567:** *Brokaw 567* (ACU), 37.63795, −118.63873, 2247 m; KM043522, KM043575. **B568:** *Brokaw 568* (ACU), 37.62344, −118.81859, 2136 m; KM043530, KM043576. **B569:** *Brokaw 569* (ACU), 37.70919, −118.95180, 2313 m; KM043523, KM043577. **B575:** *Brokaw 575* (ACU), 38.12413, −119.03270, 2140 m; KM043531, KM043578. **B577:** *Brokaw 577* (ACU), 37.74922, −118.93038, 2215 m; KM043524, KM043579. **B643:** *Brokaw 643* (ACU), 37.64034, −118.93877, 2313 m; KM043525, –.

Appendix 2

Soil Chemistry Data Collected During This Study.

Sand, Silt, Clay = percent composition of sand, silt, and clay. SOM = percent soil organic matter. CEC = cation exchange capacity (meq/100 g). Salinity = salt concentration estimated as soil electrical conductivity (dS m^{-1}). Elements and compounds are measured in parts per million of the <2 mm fraction of substrate. Vouchers codes represent collection numbers for J. M. Brokaw. Populations of *Mentzelia montana* (B567 and B643) are indicated by an asterisk (*); all other vouchers are *M. monoensis.* B566 and B567 are from a mixed population of *M. monoensis* and *M. montana*, are represented by a single composite soil sample. All other soil chemistry data are reported by Brokaw (2009).

Vouchers	Sand	Silt	Clay	SOM	CEC	pH	Salinity	B	Ca	Cu	Fe	K	Mg	Mn	Na	NO_3	P	S	Zn
B547	96	4	0	1	1.7	6.3	0.08	0	209	1.1	5.8	32	18	0.8	3	4	18	5	0.7
B550	92	8	0	1.3	2	6.9	0.08	0.1	280	0.8	4.8	70	43	2.7	6	3	23	6	0.5
B556	98	2	0	1.6	4.1	6.6	0.13	0.2	698	1.1	16.5	120	35	4.6	9	7	53	6	2.5
B557	100	0	0	0.7	4.4	7.7	0.13	0.6	535	0.5	16.6	354	84	1.8	34	4	15	7	0.3
B558	94	6	0	1.3	2.7	6.5	0.1	0.1	316	0.8	19.2	127	46	1.9	4	5	27	5	4
B559	90	10	0	0.7	2.3	5.8	0.09	0.1	204	0.8	10	67	39	3.6	6	4	14	5	0.6
B560	98	2	0	1.1	1.4	6.2	0.07	0.1	140	0.7	8.3	51	18	2	2	3	10	4	0.4
B562	100	0	0	1.3	4.4	8.1	0.16	0.3	676	0.9	6.5	102	70	2.4	42	8	6	7	0.6
B572	100	0	0	1.7	2.4	5.9	0.09	0.1	257	0.7	17	50	22	4.3	3	4	18	5	0.8
B573	98	2	0	0.5	8.8	8.4	0.16	0.2	1703	1.4	7.5	39	22	2.5	6	3	7	9	1.1
B634	100	0	0	1	3	8	0.09	0.2	504	0.7	4.4	66	39	1.7	5	3	7	5	0.4
B636	92	8	0	3.4	6.1	5.5	0.16	0.2	611	1.5	30.3	88	50	8.3	7	10	40	7	3.5
B645	94	6	0	1.3	4.5	7.1	0.14	0.1	646	1.5	13.4	94	97	3.3	46	4	16	5	1.6
B647	98	2	0	0.7	1.1	6.3	0.07	0	83	0.7	4.6	40	25	0.8	5	3	18	5	0.5
B566, B567*	86	14	0	1.7	1.6	6.2	0.07	0.1	162	1.1	5.7	78	22	1.8	4	3	11	4	0.9
B643*	88	12	0	2.2	8.3	5.7	0.2	0.1	621	1	32.5	145	92	3.9	20	12	171	8	2.4

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VEGETATION CHANGE FOLLOWING THE FOREST RESERVE HOMESTEAD ACT OF 1906 IN THE APPLEGATE RIVER WATERSHED, OREGON

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Abstract

Vegetation structure, composition, and community patterns on the landscape of southwest Oregon have changed since Euro-American settlement began in the mid-1800s. Much of this change has been attributed to the transition of land management strategies from those dominated by Native American practices, through the early Euro-American settlement period, and on to the post World War II era of industrial scale timber harvest and fire suppression. Using homestead patent applications and associated land classification maps generated under the Forest Reserve Homestead Act of June 11, 1906, we add to the understanding of historic vegetation conditions and evaluate vegetation change over time for land applied for by homesteaders in the Applegate River watershed of southwest Oregon. These homesteads were predominately located on areas now supporting chaparral, *Pinus* and/or *Quercus* woodlands, mixed conifer forests, pastures, and agricultural land. Our study presents primary source documentation that describes stands dominated by broadleaf trees and shrubs as dense at the time of patent application, contrary to the assumption that such stand structures are an artifact of fire suppression efforts of the last century. Historic vegetation polygons cross tabulated with current classified imagery in GIS indicate that conifer forests and shrublands each retain most of their former extents within their same locations on the landscape. The persistence of shrub stands to current times implies longer-term stability of these communities and indicates that a transition to conifer domination is not evident in all shrublands.

Key Words: Chaparral, grasslands, historic vegetation, oak woodlands, southwest Oregon.

The condition of shrubland and woodland vegetation of the interior valleys and adjacent slopes of southwest Oregon at the turn of the 20th century is thought to be very different from the vegetation we see today. The removal of native peoples and subsequent settlement by Euro-Americans disrupted historic human influences on the land, altered natural processes, and introduced new patterns of human disturbances. Few published studies address the effect these disruptions had on the patterns of vegetation across this landscape (Hosten et al. 2007; Duren et al. 2012). Using homestead patent applications and associated land classification maps generated under the Forest Reserve Homestead Act of June 11, 1906, we add to the understanding of historic vegetation conditions and evaluate vegetation change over time for 36 parcels of land applied for by homesteaders in the Applegate River watershed of southwest Oregon.

Under the Forest Reserve Homestead Act of 1906, settlers were able to submit homestead patent applications for lands within the newly created Forest Reserve (Gates 1913). In the Applegate River watershed this occurred between 1907 and 1918. Applications were submitted to the United States Forest Service, which was required to examine the land in question and document its vegetation cover and agricultural potential. Forest Service rangers and land examiners employed by the U.S. government produced survey reports that classified, described, and mapped the vegetation cover to scale within the surveyed boundaries of the homestead applications (USDA Forest Service 1907). Through the use of this primary source information we were able to describe the composition and structure of the vegetation, and determine the influences homesteaders had on lands applied for under the Forest Reserve Homestead Act in the Applegate River watershed. The vegetation composition maps that accompanied these homestead applications allowed us to perform a direct site comparison to observe coarse vegetation changes over the past century.

The homestead applications that we examined were of lands that are currently administered by the Bureau of Land Management (BLM) or adjacent private lands. It is a widely held assumption by many land managers, natural resource scientists, and members of the public that the characteristic state of low and middle elevation conifer and non-conifer communities of southwest Oregon prior to the onset of effective fire suppression in the last century was that of grasslands, *Quercus* L. savannas, and *Pinus* L./*Quercus* woodlands of open character (Agee 1996; LaLande and Pullen 1999; Arno 2000;

USDA Forest Service 2004). These assumptions are substantiated by historic accounts such as Lindsay Applegate's 1846 description of the valley of the main stem of the Rogue River, of which the Applegate River is a major tributary, as "a great meadow, interspersed with groves of oaks which appear like vast orchards." (Walling 1884, p. 304). While this and other historic accounts from the Euro-American settlement period (Taylor 1921; Giles 1946; Drury 1957) characterize the vegetation as "open", other vegetation descriptions commonly found in primary sources imply a brushy nature to the vegetation of low and middle elevation slopes adjacent to the valleys of southwest Oregon for this same time period. Daniel Giles wrote of traveling near the town of Ruch in 1853 "for about three miles through pine timber and thick underbrush." (Giles 1946, p. 262). Several other sources (Alcorn 1855; Beeson 1858; Taylor 1921; Robbins 1933; Drury 1957; O'Donnell 1991) report similar vegetation structural conditions for around the same time period. Examinations of stand age structures, General Land Office survey notes, historic photos, and other primary source information have validated the variability of historic vegetation density and that closed canopy woodlands were common in the region during the final quarter of the 19th century (Hosten et al. 2007; Duren and Muir 2010; Gilligan and Muir 2011; Hickman and Christy 2011; Duren et al. 2012).

Fire as a disturbance on the landscape had a pervasive and extensive influence on the formation of vegetation patterns of the Applegate River watershed (Whittaker 1960; Detling 1961; Franklin and Dyrness 1988; Agee 1991; Riegel et al. 1992). While natural ignition of fire undoubtedly occurred and played an important ecological role, ethnological records for the Applegate River watershed indicate that Native Americans actively managed parts of the landscape using fire, predominately in valley bottoms and adjacent slopes and around high elevation camps (LaLande 1995; Pullen 1996; LaLande and Pullen 1999). In the nearby Rogue River valley, the Takelma people were reported to have used fire to drive game, facilitate the collection of acorns, seeds, and insects, and to maintain grasslands and open *Quercus* savannas and woodlands (Walling 1884; Sapir 1907). Fire use for similar activities was likely repeated in the Applegate River watershed, as it was throughout the Pacific states (Holmes 1990; Williams 2000; Whitlock and Knox 2002), resulting locally in grasslands and open *Quercus* and/or *Pinus* stand structures. Native American management techniques using fire would have effectively ceased when native peoples were removed from the Applegate River watershed in the 1850s (LaLande 1995). Prospectors in the Rogue River valley and elsewhere set fire to hillsides to remove vegetation and reveal mineral resources (Butler and Mitchell 1916; LaLande 1995). Early cattlemen also used fire to maintain grassy areas, clear shrublands and promote young re-growth to provide additional forage for grazing livestock (Leiberg 1900; LaLande 1995; Alvord 1996), itself a new and ubiquitous influence on the vegetation in the area. Agee (1991) reported a fire frequency of 16 years between 1760 and 1860 and 12 yr from 1850–1920 on a south-facing slope in the Applegate River watershed slightly higher in elevation from the area we examined. The modern era of fire suppression was likely not effective on a landscape scale until after World War II, when an effort of the necessary magnitude was able to be applied to the perceived threat of wildfire. Other anthropogenic disturbances of the last one hundred and fifty years of Euro-American settlement that substantially influenced the patterns of vegetation we see today include timber harvest and attempts at clearing land for agriculture. These activities were frequently mentioned in the homestead applications and survey reports we reviewed. Widespread hydraulic mining also severely altered the development of vegetation along river and stream courses at a local scale.

An analysis of woodland stand age structure conducted in the Applegate River watershed revealed a high rate of *Quercus garryana* Douglas ex Hook. establishment from 1850–1890 with a substantial decline thereafter, and, in a limited number of stands, a significant increase around 1950 in the recruitment of *Pseudotsuga menziesii* (Mirb.) Franco (Gilligan and Muir 2011). Vegetation changes in non-conifer communities of the Applegate River watershed under conditions of fire exclusion include the loss of grasslands and open *Quercus* communities and transition to shrublands and/or closed canopy woodlands; the gradual accumulation of long-lived hardwood trees (e.g., *Quercus garryana*) in chaparral; and the accumulation of conifers in more mesic stands dominated by hardwoods (Hosten et al. 2006). The rate at which this transition to closed canopy conditions occurs is related to edaphic and other environmental conditions (Pfaff 2007).

Our objectives were to (1) evaluate the influence of homesteaders on the vegetation of middle to low elevation slopes of the Applegate River watershed through the period of the Forest Reserve Homestead Act, (2) describe the historic vegetation at the time of mapping, and (3) observe vegetation change between the time of mapping and the present. To meet these objectives we collected historical accounts from homestead applications and land classification surveys and imported into a GIS (Geographic Information System) (ESRI 2005) the spatial

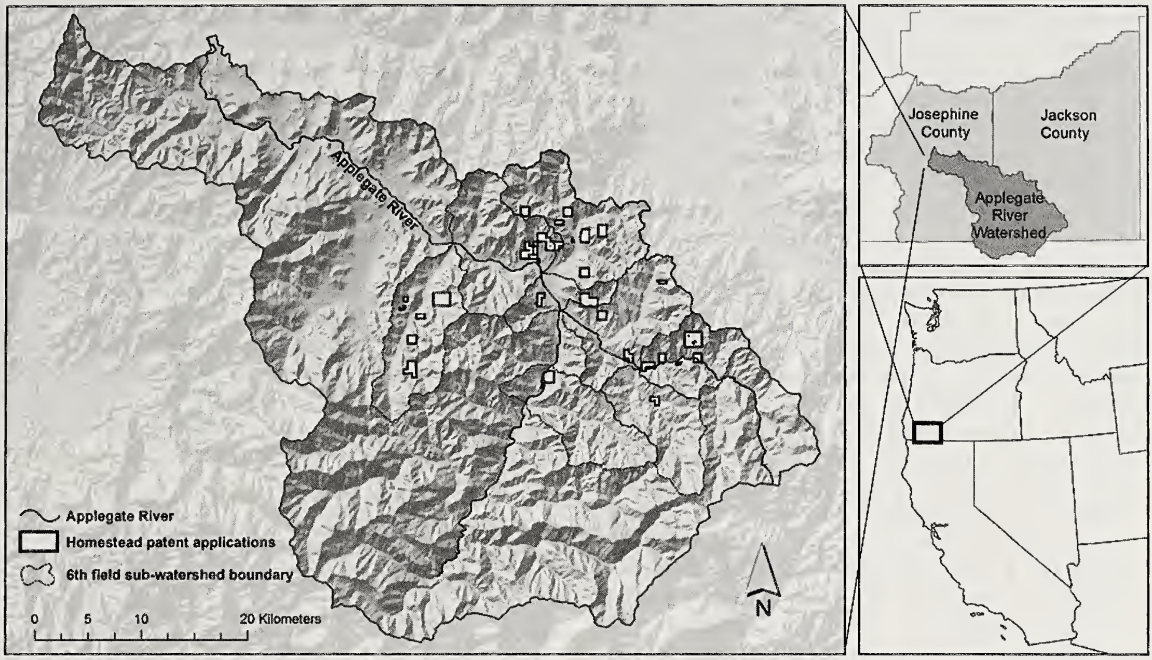

FIG. 1. The Applegate River watershed and the study area as shown by the extent of the homestead patent applications. 6th field sub-watersheds that contain homestead parcels are outlined.

information provided in the historic vegetation composition maps and compared it with current classified imagery.

METHODS

Study Area

The Applegate River watershed, located in southeast Jackson County and southwest Josephine County, Oregon (Fig. 1), is an interior valley located between the Cascade Range and the Siskiyou Mountains. The valley bottom along the main stem of the Applegate River and larger tributaries is broad, flat, and composed of alluvial soils. The foothills and mountains are characterized by steep slopes, deeply dissected drainages, and somewhat level ridgetops. The climate in the region is generally described as Mediterranean due to mild wet winters and hot dry summers. Conifer forests predominate at middle to high elevations and north facing slopes and in moist drainages at lower elevations. Meadows, chaparral, *Quercus* savannas, and *Quercus* and *Quercus/Pinus* woodlands occur at low to middle elevations on lower slopes, south facing aspects, valleys, and foothills; areas heavily influenced by serpentine geology; and on steep, south facing aspects with shallow, gravelly clay loam soils where droughty conditions limit the accumulation of conifers. At the tops of some mountains and ridges are prairies ringed by scattered *Quercus* clumps or bands of *Quercus* woodlands (Hosten et al. 2007).

These 36 parcels of land applied for under the Forest Reserve Homestead Act were selected as the extent of the study area because they represented the majority of the most complete homestead applications and survey reports available for review, and were the most concentrated spatial grouping of homesteads occurring within a large and discrete watershed that can be uniformly described. The Applegate River watershed is often treated as a discrete geographic unit in historical documents as well as by present day land managers and researchers, and therefore offers ready comparison with other studies and descriptive efforts of historic vegetation. Homestead parcels cover 2516 ha located within just eight of the 29 6th field sub-watershed units in the Applegate River watershed. This is roughly 1% of the total area of the Applegate River watershed and 3% of the 6th field sub-watersheds examined (Fig. 1).

Historical Accounts

To describe the historic vegetation at the time of mapping and evaluate the influence of homesteaders on the vegetation, we searched Forest Reserve Homestead Act applications within the Applegate River watershed that contained vegetation composition maps (Fig. 1). These were archived at the Bureau of Land Management

Medford District Office. Vegetation descriptions and ancillary information about Euro-American influence on vegetation were summarized. To compare historic and current vegetation, land classification maps were scanned and converted to digital images, which were imported and georeferenced in GIS (Fig. 2). For each map, polygons were drawn around the cover types delineated by the Forest Service surveyors. Polygons representing similar cover types based on surveyors' descriptions were grouped together and given consistent labels across all maps. Historic vegetation designations were assigned vegetation class names that coincided with the classes in the WODIP (Western Oregon Digital Imagery Project) classified imagery (Nighbert et al. 2000) (Table 1). Homestead application maps were compared with a topographic site index to determine their slope position (Jenness 2006).

Data were examined at two scales: the entire Applegate River watershed and 6th field subwatershed hydrologic units. To compare historic to current vegetation cover, the degree to which vegetation classes had changed between the time of the original mapping and recent time was evaluated. Two independent evaluations of vegetation change were conducted that compare historic vegetation maps with current information: a cross tabulation by area and a presence/absence assessment.

Cross tabulation by area. Historic vegetation maps were compared directly to recent (1993) WODIP classified imagery with similar vegetation classifications in GIS. In order to compare the historic vegetation polygons created in GIS with the WODIP data, the polygons were converted to rasters with 30 m^2 grids. Cross tabulation by area was completed at both the Applegate River watershed and 6th field subwatershed scales using the Tabulate Area function in Arc Toolbox (ESRI 2005). This calculated the amount of area of the historic vegetation classes that intercepted with present vegetation classes in WODIP. Results were displayed as a percent of the total area of a historic vegetation class that is now occupied by a current vegetation class based on 30 m^2 grids.

WODIP vegetation classes that correspond to historic vegetation classes are displayed in Table 1. The Non-forest Vegetation class in WODIP is defined as encompassing all other native vegetation that is not forest. Hardwood Woodland, Shrubland, and Grassland were analyzed as separate historic vegetation classes, though together they are equivalent to the Non-forest Vegetation class in WODIP. Visual observation of WODIP overlaid with 2005 orthophotos showed that the Non-forest Vegetation class encompassed shrublands, hardwood woodlands, and grasslands as seen in the orthophotos. However, the few areas visually interpreted to be current grasslands within the extent of historic maps were grassy balds that did not occupy the same topographic position as grasslands depicted in the historic maps. Much of the area within the extent of historic maps classed as Non-forest Vegetation in WODIP was, through visual examination, determined to be shrublands or hardwood woodlands. The interpretation of our results reflects this understanding of the WODIP information. Imperfect spatial alignment of historic maps when brought into GIS, the coarseness of the original vegetation mapping by Forest Service surveyors as well as the coarseness and misidentifying of grids in WODIP provide us with historic and current maps that are approximations of the extent of vegetation classes.

Presence/absence. Two assessments of the presence or absence of vegetation classes were completed by visual comparison with digital orthophoto quadrangles (obtained under multiagency contract with USGS, most images from 2005) to determine whether historic vegetation classes still occurred within the extent of the homestead parcel and within the extent of the historic vegetation polygon. First, for each vegetation class present within the boundaries of the homestead parcel on the historic map, we noted whether that same vegetation class was present or absent within those same boundaries in the 2005 orthophoto. Second, we noted whether current vegetation classes were present or absent within the extent of each historic vegetation polygon. This overcame some of the limitations in information classes provided in WODIP, particularly in regard to grasslands being grouped with shrublands and hardwood woodlands in the Non-Forest Vegetation class. The current vegetation class "Conifer Woodland" was added for this analysis and is comparable to the *Pinus ponderosa* Woodland vegetation class used in historic classifications.

Results

The majority of the area of the 36 Forest Reserve Homestead Act homestead parcels examined was located on middle (62%) and lower (20%) slopes (Fig. 3). Out of the total area of 2516 ha examined, the historic vegetation class that was described by surveyors to cover the greatest extent was Shrubland at 1250 ha followed by Conifer Forest at 684 ha (Table 1).

Historic Accounts

Vegetation descriptions of lands sought under the Forest Reserve Homestead Act use a preponderance of descriptors indicating dense nonconifer vegetation (Table 2). Of the 36 homestead

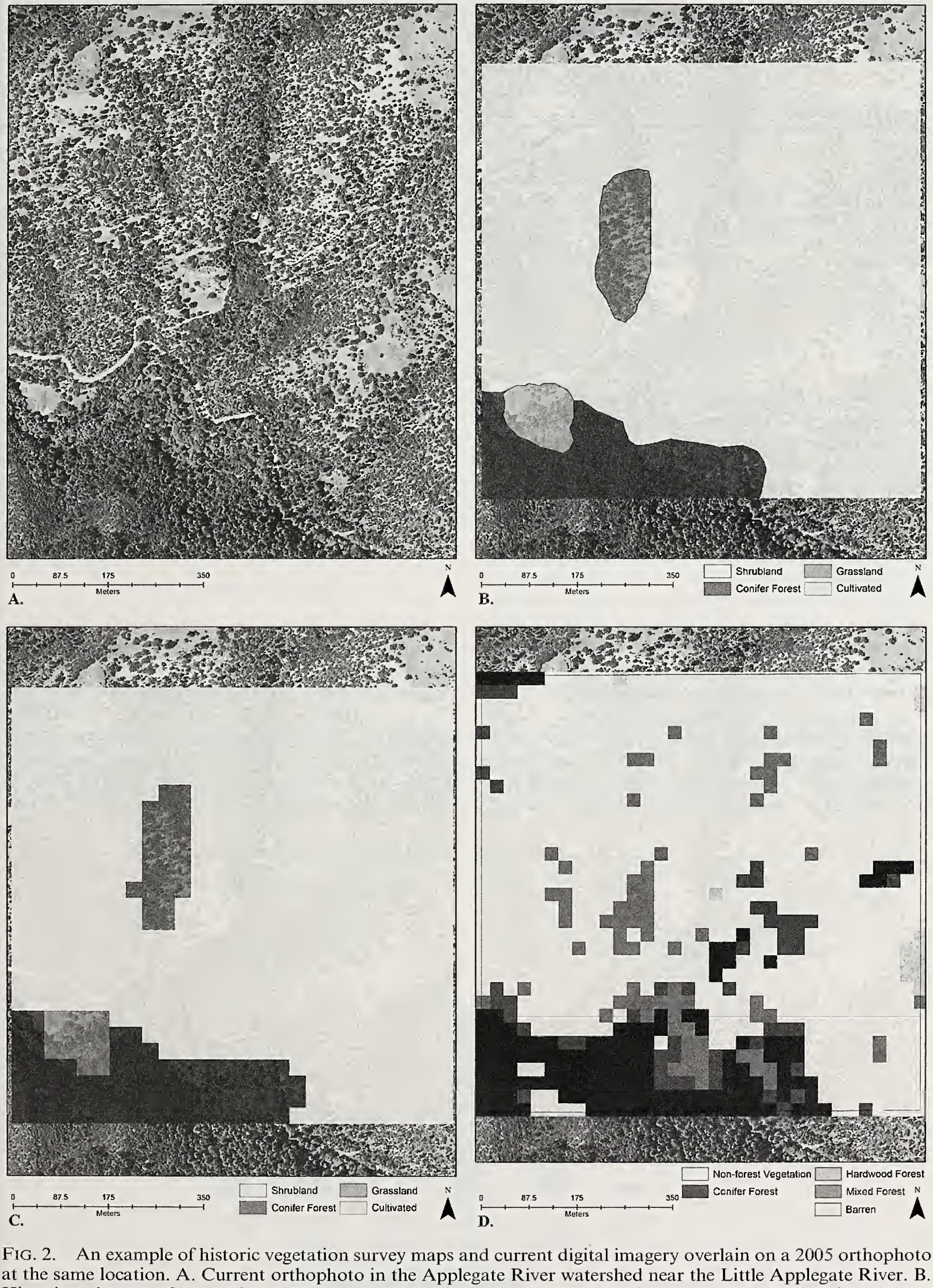

FIG. 2. An example of historic vegetation survey maps and current digital imagery overlain on a 2005 orthophoto at the same location. A. Current orthophoto in the Applegate River watershed near the Little Applegate River. B. Historic polygons of vegetation classes that were delineated by Forest Service surveyors. C. Historic polygons converted to raster data. D. WODIP digital imagery.

TABLE 1. VEGETATION CLASSES AND THEIR TOTAL EXTENT WITHIN THE STUDY AREA. Historic vegetation designations were grouped and assigned vegetation class names that coincided with the classes in WODIP.

Historic vegetation classes	Area (ha)	Historic vegetation classes comparable to WODIP vegetation classes	WODIP vegetation classes
Barren	16.8	Barren	Barren
Burn	5.3	Burned	N/A
Conifer Forest	684.4	Conifer Forest	Conifer Forest
Conifer Hardwood Forest	26.2	Mixed Woodland/Forest	Mixed Forest
Ponderosa Pine Woodland	38.2	Mixed Woodland/Forest	Mixed Forest
Cultivated	231.4	Cultivated	Urban-agriculture
Grassland	47.7	Grassland	Barren/Non-forest Vegetation
Hardwood Woodland	128.4	Hardwood Woodland	Hardwood Forest/Non-forest Vegetation
Shrubland	1250.4	Shrubland	Non-forest Vegetation
Unidentified	87.2	Unidentified	N/A
Study Area	2516		

applications, 72% mention the presence of brush or chaparral, with frequent references to the high density of the vegetation. Most homestead patent applications were located away from the main stem of the Applegate and Little Applegate Rivers, often on toe-slopes leading to higher elevations and in small drainages among foothills. This places the plant communities described predominantly on lower to middle elevation slopes. Comparable vegetation types were described at similar locations in the vicinity of the Applegate River watershed in Natural Resource Conservation Service soil surveys for Jackson County (Soil Conservation Service 1993).

In addition to clearing and cultivating, homesteaders affected these parcels and adjacent land through grazing livestock. Of all 17 claims that were reported to have livestock, 16 had at least two domestic ungulates grazing on them. Of these 16 claims, nine had more than eight animals on the property, mostly a mix of horses, cattle, hogs, sheep, and goats, and five of those nine claimants had herds of 20 animals or more. All but one of these five claimants grazed livestock on the claim as well as on the Forest Reserve under permit with the Forest Service.

Cross Tabulation by Area

Change in vegetation composition class area was calculated at two watershed resolutions, the Applegate River watershed and the 6th field subwatershed level. At the Applegate River watershed resolution, 61% of historic Shrubland remained in the Non-forest Vegetation class (Table 3). Much (33%) of the remaining historic Shrubland was classified by WODIP as a forest class, most (20%) of which is Conifer Forest.

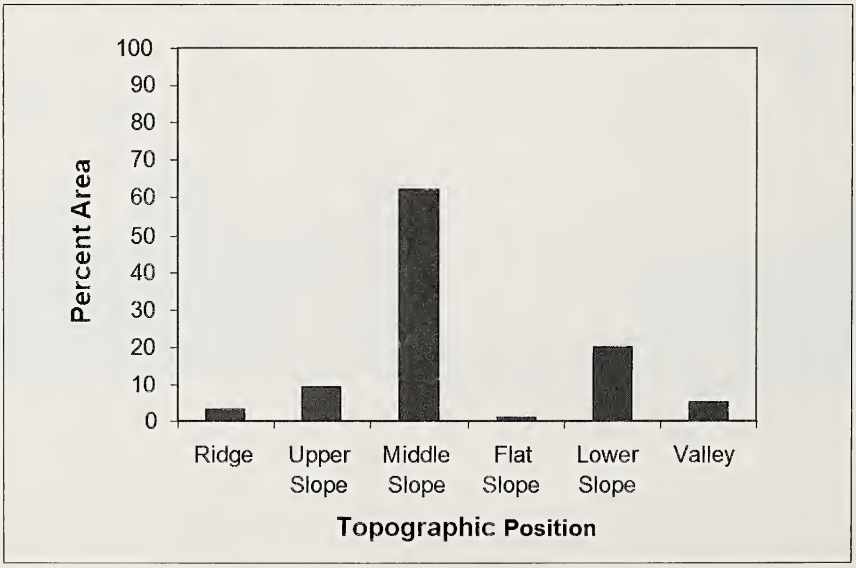

FIG. 3. Homestead patent applications cross-tabulated by area with a topographic position index. Results displayed as a percent of total homestead area that occurred in topographic position categories.

TABLE 2. KEYWORD VEGETATION DESCRIPTIONS FROM FOREST RESERVE HOMESTEAD ACT HOMESTEAD PATENT APPLICATIONS. Underlined keywords indicate sites with shrubs as a component of the vegetation. Application descriptions are separated by a period.

Township and range	Keyword vegetation descriptions
T. 38S, R. 3W, Section 8	Heavy timber; scattering timber; heavy black oak and madrone; tillable land with scattering timber.
T. 38S, R. 3W, Section 10	Under cultivation; cleared but not under cultivation; 2–15 yellow pine and Douglas fir 8″–24″ DOB and yellow pine and Douglas fir 12″ to 20″ tall 20 to 300 per ac - 1000 B.M.; manzanita, madrone and oak on most of areas dense. 1500 ft per ac yellow pine and Douglas fir; 2000 ft per ac yellow pine and Douglas fir; yellow pine reproduction; chaparral and manzanita.
T. 38S, R. 3W, Section 13	Cleared; chaparral; conifer forest.
T. 38S, R. 3W Section 14	Young growth fir 4 to 10 ft high; dense brush consisting principally of chaparral, grub oaks, and manzanita. Oregon oak, madrone, manzanita, scattering pine and fir.
T. 38S, R. 3W, Section 16	Cultivated; cleared; brush. Dense growth reproduction yellow pine; dense growth of manzanita and chaparral.
T. 38S, R. 3W, Section 20	Chaparral and manzanita brush; open; yellow pine and Douglas fir reproduction; scattered yellow pine 1200 ft per ac; barren rocky. Scattering white oak; good reproduction of yellow pine and Douglas fir; scattered yellow pine 10,000 ft B.M.; dense growth of oak grubs, manzanita, and chaparral. Chaparral and manzanita brush; Burn - 1915 - not restocking; scattering oaks grubs; scattering timber and reproduction (yellow pine and Douglas fir). Cultivated; chaparral; cleared.
T. 38S, R. 3W, Section 22	Chaparral and manzanita; open and scattering brush; under cultivation; yellow pine and Douglas fir reproduction. Brush; grass; timber-less than 2000 BF.
T. 38S, R. 2W, Section 26	Cleared and cultivated; fir; yellow pine, madrone. Farm; open land; underbrush; brushy side hill; high brushy ridge; Timber.
T. 38S, R. 2W, Section 34	Brush; grass; timber-less than 2000 BF.
T. 39S, R. 2W, Section 13	Chaparral and scrub oak; maple, white oak, black oak, birch, ash; under cultivation; grassland.
T. 39S, R. 2W, Section 20	Grassland - glade; chaparral - scattered pines.
T. 39S, R. 2W, Section 22	Brush; timber - less than 2000 B.F.; cultivated.
T. 39S, R. 2W, Section 24	Brush; grassland; old cuttings; timber; cultivated.
T. 39S, R. 3W, Section 1	Chaparral, scrub oak, manzanita; cultivated; grasslands - parks.
T. 39S, R. 3W, Section 4	One ac slashed; 10 ac cleared; One ac in orchard; 120 ac of timber.
T. 39S, R. 3W, Section 12	Dense chaparral; brush; open.
T. 39S, R. 3W, Section 14	Brush; open.
T. 39S, R. 3W, Section 28	Alfalfa fields; rocky gravel bars and rock bluffs; steep rocky ridges and mostly covered with young growth.
T. 39S, R. 4W, Section 6	Manzanita and chaparral; brush very dense also some white oak grubs; cultivated.
T. 39S, R.4W, Section 8	Timbered side hill 20,000 ft B.M. per ac; small underbrush; woodland; cultivated, garden ground.
T. 39S, R.4W, Section 14	Brush; cultivated; poles, woodland; grassland; water.
T. 39S, R.4W, Section 18	30 ac 26,500 ft B.M. to ac; 50% yellow pine 50% red fir; cultivated; brushy; poles, cordwood; grassland.
T. 39S, R.4W, Section 30	Brush; 60% fir, 40% yellow pine; clearing. Chaparral and manzanita 60% fir 40% yellow pine.
T. 40S, R.2W, Section 4	Chaparral or brush; cultivated; slashing; 250,000 ft B.M. 65% yellow pine 35% fir. 200,000 B.M. 60% fir, 30% pine, 10% cedar; cultivated.

Conifer Forest retained much of its historic area, with 54% still classed as Conifer Forest. While 13% of the historic Conifer Forest area was classed as Mixed Forest in WODIP, much of the remainder (24%) was classed as Non-forest Vegetation.

The 6th field sub-watershed analysis examined vegetation change at a more local scale (Table 4). Most sub-watersheds exhibited the same pattern as the Applegate River watershed analysis of only modest change in the amount of area within homestead parcels historically occupied by Conifer Forest and Shrubland. However, two sub-watersheds (Forest Creek and Thompson Creek) displayed an increase in current Conifer Forest area within the area historically occupied by Shrubland. Another two sub-watersheds (Humbug Creek and Middle Little Applegate) displayed an increase in current Non-forest Vegetation area within the area historically occupied by Conifer Forest. These changes in area over time were a transition towards the most extensive vegetation

TABLE 3. CROSS TABULATION RESULTS FOR THE APPLEGATE RIVER WATERSHED. Results are displayed as a percent of the total extent of historic vegetation classes that overlap WODIP classified vegetation classes (e.g., 24% of the extent of historic Conifer Forest is classed as Non-forest Vegetation in WODIP).

Historic vegetation classes	WODIP vegetation classes					
	Barren	Conifer Forest	Hardwood Forest	Mixed Forest	Urban-agriculture	Non-forest Vegetation
Barren	3	3	7	3	2	75
Burned	0	17	12	29	0	42
Conifer Forest	1	54	5	13	4	24
Mixed Woodland/Forest	1	29	5	28	2	36
Cultivated	1	18	3	5	45	26
Grassland	0	6	4	4	38	46
Hardwood Woodland	1	45	2	13	9	30
Shrubland	1	20	5	8	5	61

class currently within the sub-watersheds as depicted by WODIP.

Throughout the entire study area, 45% of historic Cultivated area remained cleared (Table 3). While this represents the greatest percentage of any vegetation class that currently occupies historically cultivated land, a larger amount (53%) of this area is now occupied by native vegetation types represented by all the remaining vegetation classes in WODIP. Non-forest Vegetation was the largest component of these combined vegetation classes at 26%, followed by Conifer Forest at 18%.

Most native grasslands mapped by Forest Service surveyors were located on lower slopes, in valley bottoms and at the confluence of streams at low to middle elevations. Much of the extent of this historic vegetation class was now occupied by Non-forest Vegetation (46%) or Urban-agriculture (38%) (Table 3). Within the extent of historic polygons classed as Hardwood Woodland, 30% was classified in WODIP as Non-Forest Vegetation and two percent classified as Hardwood Forest. The majority of historic Hardwood Woodland area (45%) was classified in WODIP as Conifer Forest and 13% was classed as Mixed Forest.

Presence/Absence Assessment

The first presence/absence assessment compared 36 individual homestead maps with 2005 orthophotos. These comparisons showed that 86% of homesteads had retained historic Conifer Forest, 68% had retained Shrubland, and 90% had retained historic Cultivated area (Table 5). However, nine out of 12 homestead parcels with historic Grassland no longer contained grasslands and 72% of homesteads contained Hardwood Woodland where it was not reported historically (Table 5).

TABLE 4. CROSS TABULATION RESULTS FOR SUB-WATERSHEDS. Numbers in bold show changes in historic to current vegetation cover. Results are displayed as a percent of the total extent of historic vegetation classes that overlap WODIP classified vegetation classes.

Sub-watershed	Historic vegetation classes	WODIP vegetation classes					
		Barren	Conifer Forest	Hardwood Forest	Mixed Forest	Urban-agriculture	Non-forest Vegetation
Forest Creek	Conifer Forest	0	55	5	15	0	24
	Mixed Woodland/Forest	1	34	3	32	0	29
	Cultivated	1	3	9	10	47	31
	Shrubland	0	**51**	2	7	3	37
Thompson Creek	Conifer Forest	0	67	4	10	4	16
	Cultivated	1	18	2	8	64	8
	Shrubland	1	**33**	5	**12**	7	43
Humbug Creek	**Conifer Forest**	1	25	8	22	1	**42**
	Mixed Woodland/Forest	1	11	4	18	6	61
	Cultivated	2	1	14	5	54	24
	Shrubland	0	15	7	15	6	57
Middle Little Applegate	**Conifer Forest**	2	35	3	4	3	**52**
	Cultivated	2	11	2	3	41	41
	Shrubland	2	11	7	5	2	73

TABLE 5. THE NUMBER OF HOMESTEAD APPLICATIONS, OUT OF 36, IN WHICH A PARTICULAR VEGETATION CLASS WAS ENCOUNTERED.

Vegetation class	Historic map only	Historic map and 2005 orthophoto	2005 orthophoto only	Neither
Barren	2	0	0	34
Burn	1	0	0	35
Conifer Forest	3	19	12	2
Conifer Hardwood Forest	1	1	25	9
Pinus ponderosa Woodland	2	1	2	31
Cultivated	2	20	5	9
Grassland	9	3	2	22
Hardwood Woodland	1	6	21	8
Shrubland	9	19	6	2

The second presence/absence assessment examined current vegetation classes within the extent of historic vegetation polygons (Table 6). The comparisons showed that Conifer Forest, Shrubland, and Cultivated vegetation classes have predominantly retained their occurrence within the boundaries of their historic mapped extents. However, the presence of different vegetation classes within these historic vegetation polygons reflected some change in vegetation cover. Among historic Grassland polygons, 85% no longer contained grasslands, and Conifer Forest commonly occurred within historic Hardwood Woodland polygons (Table 6).

DISCUSSION

The homestead patent application process as applied to the Applegate River watershed favored certain topographic locations on the landscape. Homestead application maps compared with a topographic site index showed that most of the area of homestead parcels was located on middle and lower slopes. Only five percent of the total mapped extent of homesteads was located in a valley, reflecting the fact that much of the valley bottom land in the Applegate River watershed had already been claimed and occupied by earlier settlers by the time claims were being made through the Forest Reserve Homestead Act. The presence of these earlier settlers most likely had an effect on the vegetation of the lands examined in this study in a number of ways, including the grazing of free ranging livestock, incidental burning from fires started lower in the watershed, isolated logging, and perhaps some placer mining activities (LaLande 1995). In addition to the unavailability of valley bottomland, homesteading rules compelled applicants to avoid sites with considerable stands of timber, though exceptions did occur. The following descriptions of homestead activities and vegetation change are generally restricted to lower and middle elevation slopes that had a low abundance of conifer trees.

Euro-American Disturbance

It was clear through examination of written accounts that the settlers of this time period were not always the first non-indigenous people to affect these parcels. Two claims had abandoned mine shafts and prospect holes on them. Another had a clearing and cabin that predated the claimant. The surveyor noted that the clearing

TABLE 6. THE NUMBER OF HISTORIC POLYGONS OF EACH HISTORIC VEGETATION CLASS IN WHICH CURRENT VEGETATION CLASSES OCCURRED. Numbers in bold show vegetation changes.

Vegetation class of historic polygons	Current vegetation classes							
	Conifer Forest	Conifer Hardwood Forest	Conifer Woodland	Cultivated	Grassland	Hardwood Woodland	Shrubland	Total polygons
Barren	1	0	0	1	0	1	2	2
Burn	1	0	0	0	0	1	1	1
Slash	1	0	0	1	0	0	2	3
Conifer Forest	28	20	3	13	0	13	19	45
Conifer Hardwood Forest	3	0	0	0	0	1	0	3
Pinus ponderosa Woodland	1	2	1	1	0	3	0	3
Cultivated	16	8	0	19	4	17	4	31
Grassland	2	8	1	9	**3**	12	5	20
Hardwood Woodland	**8**	4	0	2	2	6	3	9
Shrubland	25	21	6	17	10	34	31	52

was likely kept open by squatters, miners, and settlers that had stayed at the site over the years and speculated that the cabin was built by prospectors, evidenced by all the prospecting holes dug about the place. An old quartz mill was located on another parcel. An open grassy area on one parcel was reported as being used as a public pasture prior to the claimant filing on the property. Timber had been previously high-graded off another claim by local residents to be used for local construction.

The cross tabulation analysis of historic Cultivated land showed that a significant amount of this historic vegetation class has been retained in the Urban-agriculture class. However a slightly larger percent of the area historically classed as Cultivated is now in vegetation classes representing native vegetation types. Areas cleared on sites that remained in public ownership returned to native vegetation. The presence/absence assessments supported the cross tabulation results, which showed that most homesteads with historic Cultivated area and most historic Cultivated polygons currently contained this vegetation class.

Conifer Forest

Forest Service surveyors reported stands of young conifer reproduction on 16 out of 36 claims. Of these claims, five had stands that were described as dense. Surveyors described conifer stands on 11 claims as mature timberland and four of these were described as having a brush understory. No mention was made of the character of the understory for the rest of the mature conifer stands. However, a metes and bounds survey of one parcel recorded three times passing through open pine ridges or slopes (Whitney 1910). One additional stand of young growth conifer was reported to have a scattering of mature *Pseudotsuga menziesii* and *Pinus ponderosa* P. Lawson & C. Lawson. There were seven claims on which vegetation was characterized as brush or chaparral with scattered *Pinus* trees, one claim as brush with scattered *Pinus* and *Pseudotsuga menziesii* trees, another claim as a "thick stand of scrub oak, mixed with a few yellow pines (*Pinus ponderosa*) and yellow fir (likely *Pseudotsuga menziesii*)" (Tungate 1909), and three claims as hardwood woodlands with scattered *Pinus* trees. These results suggest a diversity of conifer structures on the patent application sites including open *Pinus* stands on ridges, regenerating stands with scattered older cohorts, and an association with a dense shrub layer. Several descriptions of shrublands mention a scattering of *Pinus ponderosa*, a structural feature lacking in many current day shrubland plant communities.

The cross tabulation results revealed that forest vegetation remained the dominant vegetation class in both historic Conifer Forest and historic Mixed Woodland/Forest polygons. Conifer Forest remained the dominant vegetation class in historic polygons classed as Conifer Forest. In historic maps with substantial area classed as Shrubland, Conifer Forest was confined to draws, similar to where conifer cover occurs today in the Applegate River watershed on middle to low elevation slopes amid a matrix of shrublands and woodlands. Other homesteads located in areas that were mostly forested 100 yr ago retained the same general cover today. The presence/absence assessments demonstrated that most homesteads with historic Conifer Forest retained this vegetation class and that conifer forests are still present within the extent of most historic Conifer Forest polygons.

Non-Forest Vegetation

Eleven claims had stands of vegetation mapped and characterized as chaparral or brush but did not indicate species. Of these, three were described as dense. Eight claims had stands described as *Quercus* scrub and/or *Arctostaphylos* Adans. chaparral, with two of these labeled dense. Three claims had stands identified as *Quercus* trees or *Quercus* and *Arbutus menziesii* Pursh trees. One additional claim mapped an area described as being covered by dense chaparral and brush with scattered *Quercus* trees. Two claims contained riparian hardwood woodlands, one consisting of *Fraxinus* L. and *Alnus* Mill. trees, the other of *Fraxinus*, *Acer* L., *Betula* L., *Quercus garryana* and *Quercus kelloggii* Newb. trees, and "an occasional wild crabapple" (Whitney 1910).

Non-forest Vegetation area remained the most extensive vegetation class within the extent of historic polygons classed as Shrubland. This is possibly due to these sites possessing the environmental conditions that tend to support non-forest type vegetation and exclude conifer trees and tall, closed canopy conditions. Moreover, the location of these sites on middle to low elevation slopes may have left them susceptible to repeated human caused disturbance, with the frequency of stand replacement disturbance and infrequency of conifer seedling survival limiting conversion to conifer forest. The presence/absence assessments corroborate this, which showed that most homesteads with historic Shrubland retained this vegetation and that shrublands are still present within the extent of many historic Shrubland polygons. This result emphasizes the constancy of many non-conifer communities.

Changes in percent cover from Shrubland to Conifer Forest and Conifer Forest to Non-forest Vegetation represented the most significant

amount of change in area for each of these historic vegetation classes. This may illustrate the dynamic nature of non-conifer communities embedded among conifer communities. The area that had undergone change to another vegetation class could represent seral states in each respective community type, their current condition dependant upon time of last disturbance. Some of the change observed could also be attributed to the coarseness of the original vegetation mapping by Forest Service surveyors and the coarseness and misidentifying of grids in WODIP.

Some of the historic extent of Hardwood Woodland remained classified as Non-forest Vegetation. However, the majority of this extent was currently classified as Conifer Forest and Mixed Forest, representing an increase in conifer trees within these polygons. In the second presence/absence analysis, patches of conifer trees were commonly observed within the extent of historic Hardwood Woodland polygons. Another observation made during the presence/absence analysis may indicate vegetation change because of a prolonged interval without a stand replacement disturbance within historic Shrubland polygons. Many areas historically classed as Shrubland now contain extensive areas of hardwood woodland, the proliferation and increased size of longer-lived hardwoods the likely result of an extended period without a stand replacing fire.

Most grasslands that were mapped by surveyors in the homestead applications were no longer present within their former extents. Much of the extent of these grasslands occurred in drainage bottoms and on adjacent benches and slopes and therefore represented already open and perhaps arable land. These were often the first places homesteaders attempted to cultivate their crops or seed to pasture grasses. There were several examples of cultivated areas embedded within pre-existing grasslands in the homesteads maps we examined. In addition, homesteaders also tended to build their homes near grasslands, further ensuring the influence by homesteaders on these grasslands.

Little mention is made of grasslands in written descriptions save one homestead claim that documents conversion of a grassland to cultivated land over ten years. Three separate claimants filed for this parcel. Forest Service surveyors visited the site on two occasions to evaluate the claim and in between these visits a claimant described the grassland in his application for listing the parcel. In 1911, the first Forest Service surveyor reported "A large natural glade traverses both forties from north to south"(Whitney 1911). A year later a claimant described "Eight or ten acres natural clearing"(Garrett 1912). Survey reports indicate that the first two claimants did not cultivate any part of the claim. By 1921 a third visit recorded that "The claim contains no open grass or meadow land," and that the current claimant had 10 ¼ acres under cultivation (Port 1921). This documented the likely scenario that the grassland described in the initial 1911 survey had been converted to agricultural land by 1921.

The cross tabulation analysis reports a prevalence of the current Urban-agriculture class in areas historically classed as Grassland. The presence/absence assessments revealed that most homesteads with historic grasslands no longer contained them. Of the three homesteads with grassland cover still present within the extent of the homestead parcel, one possessed a grassland bald that is far from the mapped position of the historic grassland, and two contained grasslands that are presently near the mapped historic grasslands though they are very small in extent and clearly show encroachment of woody vegetation.

Descriptions on two claims documented the effects of a severe disturbance on chaparral. A fire passed through these two neighboring claims three years prior to being surveyed. Both surveys reported that the chaparral on a portion of these parcels had been burned over and had since grown back to chaparral. Some interesting observations were made of land cleared by homesteaders. A portion of one parcel was recorded as "cleared, given a fair agricultural test,... now abandoned, and yellow pine encroaching from all sides"(MacKechnie 1916). Another historic account offers a testament to the persistence of oaks after clearing. "There is a great deal of scrub oak where they have cleared, which has necessitated much hard work to clear and grub"(Gribble 1912).

The influence of livestock grazing, burning by cattlemen, as well as clearing on these parcels by previous Euro-Americans inhabitants, offer alternative explanations for the existence of grasslands and open areas near drainages on the homestead parcels we examined. This is in addition to the notion that these grasslands were recently burned patches of non-forest vegetation, were edaphically controlled and maintained by fire, and/or that they owe their origin to Native American management.

Little evidence of open *Quercus* savannas was found within the homestead parcels. Vegetation may have increased in density and canopy cover prior to the Forest Reserve Homestead Act. LaLande (1995) indicates that Native American burning in the Applegate River watershed would have been concentrated at low elevations and certain high elevation sites. It is also possible that *Quercus* savanna vegetation structures were located beyond the lower to middle slope locations occupied by the homestead patent applications, were avoided by applicants, and/or were rare on low and middle elevation slopes in

the Applegate River watershed during the time of the Forest Reserve Homestead Act.

Conclusions

The unavailability of lowlands with alluvial soils favored against settlement in the broader valley bottom of the Applegate River watershed and the requirements for a successful patent application favored against settlement on lands with high timber volume. Instead, homesteaders during the time period of 1907–1918 selected lands with a high occurrence of non-conifer vegetation and stands of regenerating conifer forest. Homestead patent applications revealed that many sites showed signs of human disturbances from before the application process including mining, livestock grazing, and prior attempts at settlement.

Our results substantiated some of the presumed effects that modern fire suppression has had on this landscape. Grasslands mapped by Forest Service surveyors have been severely diminished over time. Nearly half of their historic extent is now occupied by Non-forest Vegetation consisting of mostly shrublands and hardwood woodlands, with much of the remainder converted to agricultural land. Furthermore, a shift from hardwood woodland to conifer domination occurred over a limited area.

The conversion of native vegetation to agricultural land had lasting effects on many homestead parcels, particularly the conversion of native grasslands to cultivated land. However, settlement was not always successful on this portion of the landscape. Just under half of the land area cleared historically had remained cleared; the rest had reverted to Non-forest Vegetation or Conifer Forest.

Conifer Forest has maintained much of its historic position and extent. Much of the area classed as Shrubland in historic maps remained classified as Non-forest Vegetation in WODIP. The predominant change was from historic Shrubland to Conifer Forest and historic Conifer Forest to Non-forest Vegetation. A recent study using General Land Office survey records to examine historic vegetation change of the Rogue River watershed, of which the Applegate River is a major tributary, revealed a similar pattern of change from one dominant vegetation type to another but with the transition balancing out such that the overall character of the vegetation across the landscape remained consistent over time (Duren et al. 2012).

The historic physiognomic structure of the vegetation of the area examined on low and middle elevation slopes in the Applegate River watershed was not predominantly "open" prior to modern era fire suppression efforts. Chaparral communities with a dense brushy character and closed canopy woodlands were common in areas subject to homestead patent applications and similar vegetation persists at many of these same locations at present. Many shrublands included scattered conifer trees historically. The primary sources investigated in this study did describe the vegetation of some areas as grassland and open woodland; however, the majority of the area surveyed was described as shrubland. In addition, historic conifer forests were often described as dense or having a brushy understory. The frequent occurrence of shrublands had not been well documented previously in studies of historic vegetation that included the Applegate River watershed (Hickman and Christy 2011; Duren et al. 2012).

Patent applications that were the subject of the historic surveys were heavily biased towards low and middle elevation slopes and higher up within some watersheds. Earlier historic accounts of open vegetation conditions (e.g., savannas and grasslands) were biased towards broad valley bottoms and travel corridors. Vegetation that was open and vegetation that was brushy coexisted in the historic landscape of the Applegate River watershed. These two structural types generally occurred on different geographic and topographic locations on this landscape, with the extents of each type augmented through space and time in response to broad gradients in environmental variables and natural and human caused disturbances. Reference conditions that include shrub dominated vegetation, closed canopy woodlands, and patches of conifer forest at low elevations align better with the late settlement era vegetation patterns of low and middle elevation slopes of the Applegate River watershed as described by our data and other studies (Hickman and Christy 2011; Duren et al. 2012).

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NORTHERN RANGE LIMIT OF *OPUNTIA FRAGILIS* AND THE CACTACEAE IS 56°N, NOT 58°N

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ABSTRACT

Two of the most used sources for distributions of cacti (Cactaceae) indicate the family's northern range limit is either 58°N or 58°15′N for *Opuntia fragilis*. However these sources overstate the range limit by almost two degrees, an error that probably originated as a simple misreading of the latitude of Fort St. John. I discuss records of *O. fragilis* at and just south of 56°17′ N along the Peace River valley between Fort St. John, British Columbia and Peace River, Alberta, as well as why it is surprising but unlikely that specimens currently exist farther north. An error in latitude of 2° (223 km) in range can adversely affect ability to empirically estimate effects of climate change.

Key Words: Cactaceae, *Opuntia fragilis*, range, northern latitude, climate change.

Lyman Benson in *The Cacti of the United States and Canada* claimed that the most northerly population of *Opuntia fragilis* (Nutt.) Haw. was near Fort St. John, British Columbia, Canada at either 58°15′N (Benson 1982, p. 395) or 58°08′N (Benson 1982, p. 919), depending on whether you read the legend of his distribution map or the documentation in his appendix (Fig. 1). The specific locale was along the Beatton River, 8 km (5 miles) east-northeast of Fort St. John. The 13 km (07′) difference in latitudes between the two parts of his book seemed perplexing, motivating this manuscript.

Opuntia fragilis is well-known from collections near the Peace River as it flows east from Fort St. John, through the towns of Taylor, British Columbia (15 km southeast of Fort St. John), Clayhurst, British Columbia at the Alberta border (50 km east-southeast of Fort St. John), Dunvegan, Alberta (150 km east-southeast of Fort St. John), and Peace River, Alberta (250 km east of Fort St. John) at the confluence of the Peace and Smoky Rivers. Often *O. fragilis* is found growing right along the banks of the Peace River, e.g., 6.5 km west of Taylor, British Columbia (*James A. Calder & J. M. Gillett 24599* [24 May 1960] UBC-V-119569), never far from the Peace River or its tributaries (Felix Sperling, personal communication, 14 Nov 2014), except at the badlands of Kleskun Hills. Locales along the Peace River valley are at latitudes between 55°55′N (Dunvegan) and 56°17′N (Fort St. John). The latitude of 56°17′N is 205 km south of the 58°08′N northern limit listed by Benson (1982, p. 91) and 223 km south of the 58°15′N northern limit also listed by Benson (1982, p. 395). Thus, due to probably nothing more than a clerical error, Benson (1982) stated that Fort St. John and the northernmost locale for *O. fragilis* from just outside of that town were near 58°N, not 56°N. By contrast, I have no idea where Benson's discrepancy of 58°15′N versus 58°08′N arose from, even though this discrepancy got me looking at these problems.

The herbarium sheet that Benson (1982, p. 919) identified as containing "the northernmost cactus collection", *Calder & Gillett 24615* (25 May 1960) DAO-82237, does not explicitly include latitude or longitude coordinates, but merely states, "Occasional on steep open prairie slope above river at 900′. Along Beatton River about 5 miles ENE of Ft. St. John." Any error in identifying the latitude of this specimen undoubtedly occurred in subsequently looking up or transcribing the latitude of the town of Fort St. John. This flowering specimen not only has Lyman Benson's label, but also that of Bruce Parfitt, one of the two editors of the Cactaceae section of *The Flora of North America* (FNANM) (Parfitt and Gibson 2003). Parfitt and Gibson (2003) and Benson (1982) are the two volumes containing commonly cited distribution maps of *Opuntia fragilis* (also see Staniforth and Frego 2000).

The section on *Opuntia* in *The Flora of North America* (Pinkava 2003) seems to repeat Benson's (1982) error by showing the northern range limit of *Opuntia fragilis* at around 58°N. *The Flora of North America* does not report this latitude *per se* in the text, but graphically shows the latitude on the distribution map. I took a screen capture of the distribution map (http://www.efloras.org/object_page.aspx?object_id=13216&flora_id=1; accessed 13 August 2014), then measured how far along the straight portion of the Alberta-British Columbia border, which runs along the 120th meridian from 53°48′23″N to 60°N, that the

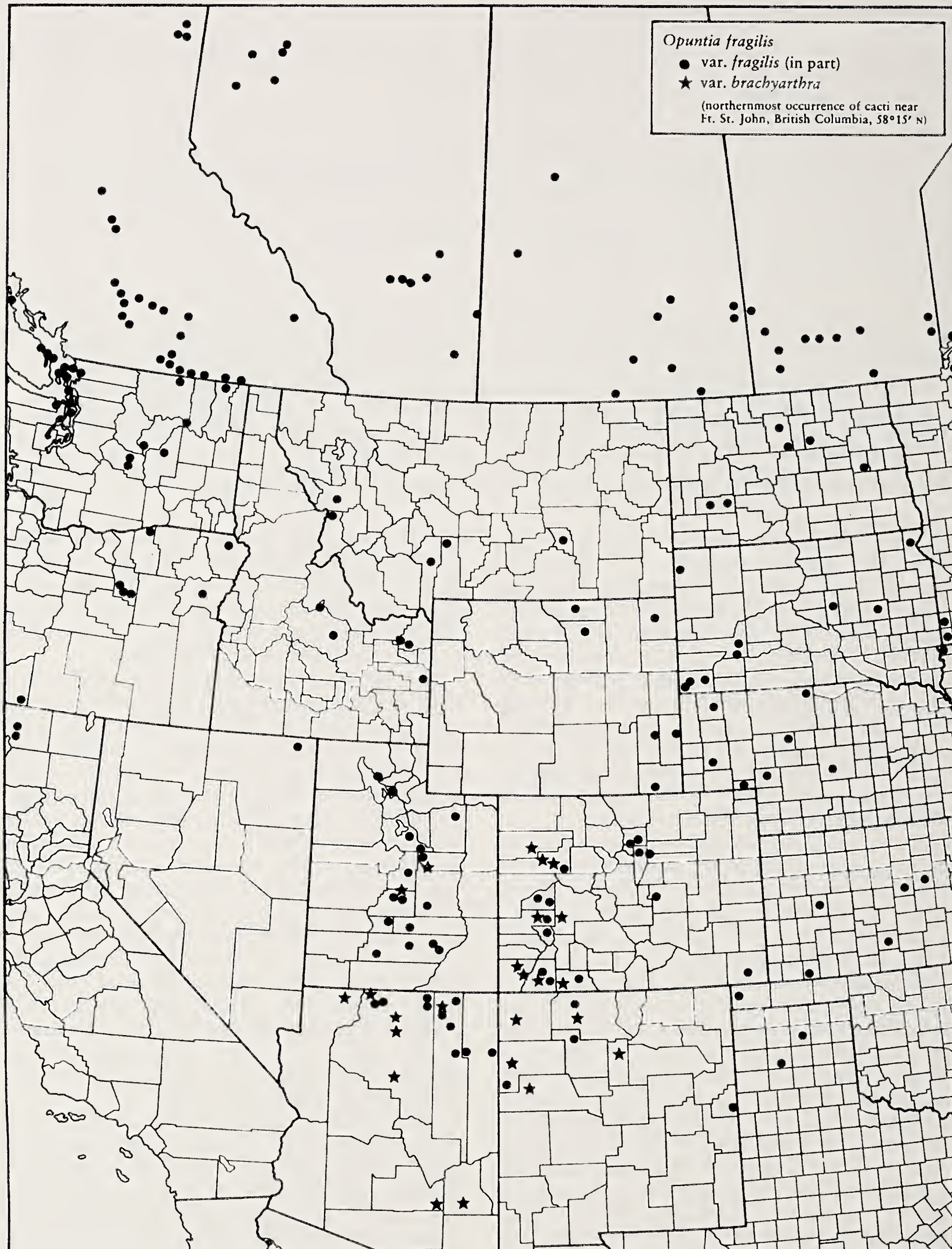

FIG. 1. Lyman Benson's (1982) distribution map of *Opuntia fragilis*, reproduced with permission of Stanford University Press. The eight northernmost dots are from the Peace River valley British Columbia and Alberta, Canada. This map does not show the eastern portion of the range, for which Benson provided a second map that included additional sites in Ontario (Canada), Minnesota (USA), Wisconsin, Michigan, Iowa, and Illinois, all of which are south of 50°N.

northern range limit appeared to be. The displayed range limit on that map is almost exactly 2° south of the Northwest Territories border, which lies at 60°N. Furthermore, the northern range limit on *The Flora of North America* distribution map seems to extend along a single latitude near 58°N, bisecting the Alberta-British Columbia border, albeit with a slight dip to the south at the provincial border, much as the Peace River does between the towns of Peace River and Fort St. John. And the east-west extent of the northern range limit on *The Flora of North America* distribution map is approximately 250 km, which is the distance between those two towns. Thus, in constructing the distribution map for *O. fragilis*, it seems that the author and editors of the *Opuntia* section of *The Flora of North America* relied on the northern range limit being around 58°N, which is wrong regardless of whether or not this information was erroneously gleaned from Benson (1982). This mean that the two most used sources to establish the northern range limit of the Cactaceae – namely Benson (1982) and Pinkava (2003) – are in error by 2° of latitude.

While not the focus of their works, other authors have also accepted Benson's (1982) erroneous northern limit of 58°N or 58°15′N for *Opuntia fragilis*, e.g., Nobel (1988), Boyle and Anderson (2002), and Ribbens (2008).

Hugo Cota-Sánchez (2002) examined many herbarium records and then wrote the definitive paper on Canadian cacti, albeit published in a small and relatively obscure journal. Cota-Sánchez (2002) recorded the correct coordinates for the most northern specimens of *Opuntia fragilis*, at 56°17′N, 120°39′W in the northeast outskirts of the town of Fort St. John. This is roughly halfway between Cecil Lake and the North Peace Regional Airport, probably just off of Cecil Lake Road. As Cota-Sánchez (2002) notes, the collection was *L.E. Pavlick & B. Taylor 79-717* (16 July 1979) V-98316, not the specimen that Benson (1982) had noted, namely *Calder & Gillett 24615* (25 May 1960) DAO-82237. My only complaints are minor regarding Cota-Sánchez's Table 1, in which he lists two herbarium specimens collected from around Fort St. John, V-98316 and V-92481, as being from Alberta (his table should say 'British Columbia'), and for the most northerly specimen, V-98316, Cota-Sánchez noted that it was located southwest of Cecile Lake (his table should say 'Cecil Lake' without the trailing 'e'). These are minor points, but there can be curious consequences of copying innocuous errors from seemingly reliable sources (Bruner 1942; Rekdal 2014a, b). Ezra Henry Moss (1959) in *Flora of Alberta* also correctly reported the northernmost latitude for *O. fragilis*, albeit from 250 km east of Fort St. John in the town of Peace River, Alberta at a locale that is negligibly farther south – approximately 2 km farther south – of the collection near Cecil Lake in Fort St. John. Moss personally collected the Peace River specimen: *E.H. Moss 6107* (17 July 1941) ALTA-12870. Table 1 lists all collections I could locate of *O. fragilis* north of Grand Prairie, Alberta, i.e., roughly from 55°N to the northern range limit at or near at 56°17′N. All of these herbarium records of *O. fragilis* in Table 1 are from the Peace River watershed and mapped on Figure 2. Figure 2 is meant as a detailed supplement to the far northern part of the distribution map provided by Benson (1982), which is reproduced herein with permission as Figure 1. The closest conspecifics to these are over 400 km away at Gibbons, Alberta, which is in the North Saskatchewan River watershed (*L.T. Lau* 44 [9 Sept 2005] ALTA-114639, Gibbons Echo Glen Park, near Sturgeon River; 53°50′N, 113°20′W) and slightly more distant locales in the Fraser River and Columbia River watersheds of British Columbia. Benson (1982) and Staniforth and Frego (2000) showed this disjunct distribution in the Peace River watershed, but Pinkava (2003) in *The Flora of North America* erroneously does not show this disjunction possibly because of the low-resolution of its range maps.

The disjunct habitat of *Opuntia fragilis* along the Peace River watershed is likely due to cacti largely needing grassland environments. The Peace River Grassland is separated from the grasslands of southern Alberta and the grasslands of the Fraser River valley of British Columbia by large swaths of forests (see figure 2 in Schmidt et al. 2014). The Peace River Grassland extends west to just beyond Fort St. John, south to Grand Prairie, and east to the town of Peace River. The northern extent of the Peace River Grassland is along the northern banks of the Peace River from just east of Fort St. John to Notikewin Provincial Park. The disjunct Peace River Grassland has been used to explain disjunct northern range limits of several plant and animal taxa (Strong and Hills 2003; Schmidt et al. 2014). Other disjunct grasslands exist further north, such as near Fort Vermillion on the Peace River (58°24′N, 116°03′W), High Level (58°30′N, 117°08′W), and the upper Yukon River valley of the southern Yukon, north of 60°N (Schmidt et al. 2014).

It is dangerous drawing inferences from negative results, but worth a try. The northern range limit of *Opuntia fragilis*, at and around 56°N along the Peace River, is bracketed by a pair of major highways: the Alaska Highway (British Columbia Highway 97) going north from Fort St. John and the Mackenzie Highway (Alberta Highway 35) going north from the town of Peace River. The Alaska Highway is the most-traveled road from southern Canada and the continental U.S. to Alaska and the Yukon. The

TABLE 1. COLLECTIONS OF *OPUNTIA FRAGILIS* NORTH OF 54°N. Herbaria: ALTA = University of Alberta; CAN = Canadian Museum of Nature; DAO = Agriculture Canada; SASK = University of Saskatchewan; UBC-V = University of British Columbia Vascular Plant Herbarium; V = Royal British Columbia Museum. A single asterisk (*) indicates that Benson (1982) examined this specimen. In June 2012, Andrew Gdaniec (personal communication, 3 Nov. 2014) recorded GPS coordinates for *O. fragilis* at Bear Flats as 56°17′N, 121°14′W (indicated with double asterisks [**]). Note that the spelling of "Beatton" has varied over time. The Beatton River, a.k.a. Beaton River, was named after Francis (Frank) Work Beatton (1865–1845), a fur trader for the Hudson's Bay Company at Fort St. John (British Columbia Geographical Names Office, n.d. (http://apps.gov.bc.ca/pub/bcgnws/names/2769.html), *inter alia* citing Harvey, 1945–1950). Further confounding matters, Frank Beatton's middle name has also been reported as "Worth". In the 1940s, his son (Frank Beaton, 1904–1973) and other family members supposedly altered the spelling of their surname to "Beaton" with a single 't' (Harvey 1945–1950). This table uses the currently accepted spelling "Beatton River", which is not necessarily the spelling on all herbarium labels. Estimated coordinates are based on Google Earth. These are my best estimates given information on herbarium labels. The northernmost latitude here of 56°18′N (V-24524) is the southernmost point on Cecil Lake, but that specimen might be from south of Cecil Lake, i.e., closer to 56°17′N. My estimate of 56°15′N for the "high slopes N of town of Peace River" (DAO-82222) is based on topography, where the highest slopes are in the northeast corner of town at around 490 m.a.s.l. The two specimens at the north side of the Beatton River crossing of Cecil Lake Road (V-34956 and V-54734) are possibly from the same locale. Localities are from specimen labels.

Locality	Estimated coordinates	Collector and collection number (collection date)	Herbarium and accession number
BC, Peace River area, Cecil Lake, near Fort St. John	56°18′N, 120°35′W	*T.B. Widdowson 5462* (6 July 1954)	V-24524
BC, Fort St. John, Beatton River, SW of Cecil Lake	56°17′N, 120°39′W	*L.E. Pavlick & E.B. Taylor 79–717* (16 July 1979)	V-98316
BC, Fort St. John, hill on N side of Cecil Lake [Road?] crossing of Beatton River	56°17′N, 120°44′W	*D.H. Calverley 185* (13 July 1958)	V-34956
BC, Beatton River breaks, E of Fort St. John on road to Cecil Lake, north side of river valley	56°16′N, 120°39′W	*T.C. Brayshaw 5329* (31 July 1976)	V-54734
BC, 5 miles ENE of Fort St. John	56°16′N, 120°39′W	*J.A. Calder & J.M. Gillett 24615* (25 May 1960)	DAO-82237*
BC, Fort St. John, Bear Flat	56°16′N, 121°10′W	*T.C. Brayshaw & C.C. Chuang 6092* (20 August 1976)	V-92481**
BC, Peace River, Alaska Hwy [near Fort St. John]	56°15′N, 120°′W	*H.M. Raup & D.S. Correll 11659* (5 Sept 1943)	CAN-280525
AB, high slopes N of town of Peace River	56°15′N, 117°17′W	*H. Groh 2792* (17 August 1946)	DAO-82222
AB, town of Peace River	56°14′N, 117°19′W	*E.H. Moss 6107* (17 July 1941)	ALTA-12870
AB, E of town of Peace River	56°14′N, 117°16′W	*N.A. Skoglund 934* (19 June 1973)	SASK-57111
AB, Peace River (town)	56°14′N, 117°18′W	*B. Heywood 206* (5 Aug 1971)	ALTA 39409
AB, Peace River, Smoky River Mission,	56°13′N, 117°17′W	*J. M. Macoun 59869* (7 July 1903)	CAN 81906*
BC, 4 miles W of Taylor Flats, N of railroad bridge	56°10′N, 120°45′W	*J.A. Calder & I. Kukkonen 26788* (10 July 1960)	DAO-82243*
BC, about 4 miles W of Taylor on N bank of Peace River	56°09′N, 120°43′W	*J.A. Calder & J.M. Gillett 24599* (24 May 1960)	DAO-82235*; UBC-V-119569; UBC-V-218942; V-051524
BC, Taylor Flat, N bank Peace River	56°08′N, 120°42′W	*H.M. Raup & E.C. Abbe 3586* (12 June 1932)	CAN-81916*
BC, Clayhurst, lot BC 2051 (I.B.P. Ecological Reserve)	56°08′N, 120°01′W	*T.C. Brayshaw 5329* (29 July 1969)	V-054735; UBC-V-218941
BC, Peace River breaks near Clayhurst Ferry	56°08′N, 120°05′W	*L.E. Pavlick & E.B. Taylor 79–519* (10 July 1979)	V-098317
BC, Clayhurst Crossing	56°07′N, 120°05′W	*A.A. Rose 78529* (2 July 1978)	UBC-V-163724
AB, Dunvegan, slopes of Peace River valley	55°55′N, 118°36′W	*B. Boivin & D. Dunbar 10568* (10 Aug 1954)	ALTA-22395; DAO-82216*
AB, Dunvegan, S slope of Peace River valley	55°55′N, 118°36′W	*E.H. Moss 7548* (20 July 1947)	ALTA-12868; DAO-82221*

Table 1. Continued.

Locality	Estimated coordinates	Collector and collection number (collection date)	Herbarium and accession number
AB, Dunvegan, S slope of Peace River valley	55°55′N, 118°36′W	*E.H. Moss 7445* (21 July 1947)	ALTA-12869
AB, Watino, Smoky River, steep dry slope	55°43′N, 117°37′W	*E.H. Moss 7690* (1 Aug 1947)	ALTA-12867; DAO-82224*
AB, Watino	55°43′N, 117°37′W	*L.C. Marvin, D. Lebedyk, G. Bilodeau, R. Serbit 3349* (4 Aug 1988)	ALTA-97013
AB, Watino, Smoky River	55°43′N, 117°37′W	*A. G. Schwartz -1033* (14 Sept 1989)	ALTA-97600
AB, Kleskun Hill, NE of Grand Prairie, dry hillside, badland	55°15′N, 118°32′W	*E.H. Moss 8120* (18 June 1948)	ALTA-12866; DAO-82218*
AB, Kleskun Hills Natural Area, N of Grand Prairie	55°15′N, 118°31′W	*R.J. Bayer, L.C. Marvin, B.G. Purdy 89016* (2 July 1989)	ALTA-102929

Mackenzie Highway is the most-traveled road from southern Canada to the Northwest Territories. Given the amount of traffic on these two highways and that most botanical collections are made along or near roads, it is noteworthy that *O. fragilis* has never been documented north of 56°17′N. Under the tab labeled 'strengths', the Royal BC Museum's botany collection website (http://royalbcmuseum.bc.ca/nh-collections/botany-plants/; Royal BC Museum, n.d.) states, "Regions of the province that can be easily accessed by road have been frequently visited by botanists over the last century, and are relatively well-represented in our collection. These regions include the southeast quarter of BC, the Alaska Highway corridor, Vancouver Island, and National and Provincial Parks." Both the Alaska and Mackenzie Highways provide seemingly suitable habitat for *O. fragilis*, especially the Mackenzie Highway as it passes through grasslands in the Notikewin River valley. The Alaska Highway remains just west of the Rocky Mountains from Fort St. John to Fort Nelson at 58°48′N. The Mackenzie Highway is parallel to and 10–15 km west of the Peace River from the town of Peace River to the town of High Level at 58°31′N. No specimens of *O. fragilis* have been collected nor even reported from either of these stretches of highway, despite decent herbarium collections from these locales. One of the anonymous reviewers wrote, "collections from 1988 and 1989 from Watino and Kleskun Hills Natural Area were made during an expedition that continued up to BC, Alaska, NWT and the Yukon. No more northerly populations of *Opuntia* were collected." The Watino and Kleskun Hills collections are *L.C. Marvin, D. Lebedyk, G. Bilodeau, R. Serbit 3349* (4 Aug 1988) ALTA-97013 and *R.J. Bayer, L.C. Marvin, B.G. Purdy 89016* (2 July 1989) ALTA-102929, respectively, both of which are listed in Table 1. Provincial and federal park staffs usually have a great notion of their floras. However, there have been no collections nor reports of *O. fragilis* from Notikewin Provincial Park, at the confluence of the Notikewin and Peace Rivers, between 57°08′N and 57°19′N, i.e., 100–120 km north of the town of Peace River (Joyce Gould, personal communication, 13 Aug. 2014). Lack of *O. fragilis* is especially noteworthy because of the extensive grasslands (much of which is farmed) along the lower Notikewin River (Schmidt et al. 2014). For these reasons, it is unlikely that *O. fragilis* is present, let alone abundant, north of 56°17′N, at least near the Alberta-British Columbia border.

Given that in the Peace River watershed *Opuntia fragilis* is largely known from slopes and dry banks closely overlooking rivers, Table 2 provides a list of places northwest of Fort St. John where existing roads cross rivers, including the Beatton River, Halfway River, and Cameron River. These might be decent places to search for range extensions of the Cactaceae. Slopes of river valleys may provide suitable habitat for cacti because of lower density plant cover and draining of water and cold air. The Beatton River should be especially promising given the extensive grasslands surrounding it (Schmidt et al. 2014). It is possible that animals transport *O. fragilis* while traveling along riparian corridors. When leaving habitats of *O. fragilis*, I always check articles of clothing for hitchhiking cladodes, which readily abscise then attach to any clothing below ankle level, hence the common name 'brittle prickly-pear' and the specific epithet '*fragilis*' (see Figure 2 in Staniforth et al. 2002). *Opuntia fragilis* does not seem to have any specific edaphic requirements, growing quite well on slopes and flat areas, in sand and in clay, as well as on granitic outcrops, even growing in dense patches of moss and lichen (Moss 1959; Maw and Molloy 1980; Staniforth and Frego 2000; Cota-Sánchez 2002). *Opuntia fragilis* is so well hidden under thick mosses and lichens near Kaladar, Ontario that the easiest way for me to relocate plants is to walk barefoot. *Opuntia fragilis* also disperses asexually when cladodes (pads) detach,

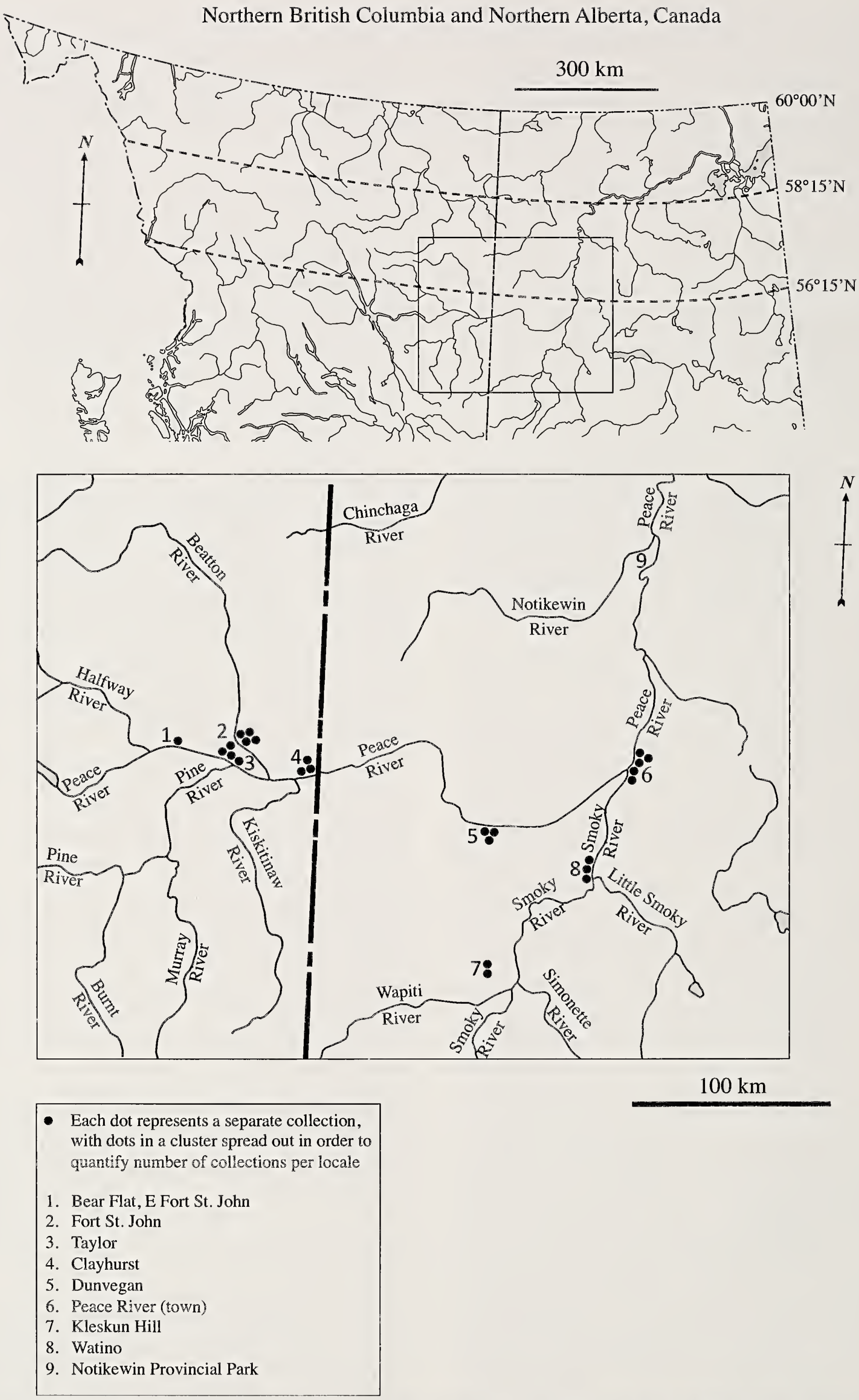

FIG. 2. Distribution map of *Opuntia fragilis* in the Peace River valley, from the herbarium records in Table 1. Underlying base map from *The Atlas of Canada* (http://atlas.gc.ca).

TABLE 2. POTENTIAL ROADSIDE HABITATS FOR *OPUNTIA FRAGILIS* NORTH (AND WEST) OF FORT ST. JOHN.

Locality		Coordinates
Beatton River road crossings:		
Beatton River Road (Mile 73 Road) crossing of Beatton River		57°17′N, 121°28′W
Tommy Lake Road (Mile 115 Road) crossing of Beatton River		57°17′N, 121°43′W
Mile 126 Road crossing of Beatton River		57°04′N, 122°08′W
Mile 135 Road parallels Beatton River		
	between	57°07′N, 122°17′W
	and	57°09′N, 122°18′W
Alaska Highway (BC 97) crossing of Beatton River		57°05′N, 122°35′W
Cameron River and Halfway River road crossings:		
Upper Halfway Road crossing of Cameron River		56°32′N, 121°48′W
Upper Halfway Road parallels Halfway River		
	between	56°30′N, 122°04′W
	and	56°28′N, 122°20′W

roll down riverside slopes, and eventually get carried downstream, where they later root near the high water mark (Frego and Staniforth 1985). Unless physically ruptured, detached *O. fragilis* cladodes had 100% survival and re-rooting after floating in an agitated flask of distilled water for 40 d (Frego and Staniforth 1985). This would explain the preponderance of records of *O. fragilis* along the Peace River watershed, implying that downstream dispersal is more common than upstream dispersal. However, specimens of *O. fragilis* have been documented upstream of the town of Taylor along both the Peace and Beatton Rivers, as well as upstream of the town of Peace River along both the Peace and Smoky Rivers. Nonetheless the lack of any records of *O. fragilis* downstream of the town of Peace River, i.e., to the north, is surprising, especially with no records from Notikewin Provincial Park. This virtually begs for a downstream canoe trip along the Peace River from the town of Peace River, searching for suitable habitats and cactus plants along the floodplain, possibly as far north as the grasslands around Fort Vermillion (58°24′N) and the grasslands along the lower Notikewin River (57°00′N–57°16′N).

There are conservation concerns for *Opuntia fragilis*, especially at what is almost the most northerly locale in the northern portions of Bear Flat, east of Fort St. John. If the Site C dam is constructed as planned on the Peace River in southwest Fort St. John, just downstream of the confluence of the Peace and Moberly Rivers, substantial potential habitats for *O. fragilis* will be destroyed. See the BC Hydro map (https://www.sitecproject.com/about-site-c/maps) for extent of flooding from this dam. Construction of the Site C dam won final approval by the British Columbia government on 15 December 2014. Not only will the Bear Flat population be inundated, but so will other potential habitats along the Peace, Moberly, and Halfway Rivers. This is of special concern because *O. fragilis* is only found very close to the Peace River and its tributaries this far north, with the only known exception being the Kleskun Hill plants at 55°15′N.

It is highly unlikely to find more northerly cacti far to the east of the Rocky Mountains simply because winters are colder and wetter in the Canadian prairies (see Agriculture Canada's cold hardiness maps at http://www.planthardiness.gc.ca/?m=1; Natural Resources Canada, n.d.). Benson's (1982) distribution map only includes one specimen from the prairies north of 52°N, which is from the vicinity of Battleford, Saskatchewan (town at 52°45′N, 108°20′W). Consistent with this, Hancock (2013) notes that the most northern cactus in Saskatchewan is *Opuntia fragilis* from just east of Battleford, which is also consistent with the distribution map in *The Flora of North America* (Pinkava 2003). The Canadian Rockies themselves are of sufficiently high elevation to lack cacti. But the Pacific coast of Canada and the Alaskan panhandle, with their moderate temperatures due to the Kuroshio Current, may, in theory, have specimens of *O. fragilis*, a species that is relatively common just above sea level near the U.S.-Canadian border along Puget Sound and the Strait of Georgia. Benson (1982, p. 397) stated that *O. fragilis* is "reportedly on rocky headlands of southernmost Alaskan islands in situations similar to those along Puget Sound, but not found there during a special search in 1959." Even if the southernmost islands in Alaska were to have *O. fragilis*, this would still be south of Fort St. John and the town of Peace River. The southernmost point in Alaska is on Dall Island at 54°40′N and even Ketchikan is at 55°22′N. Benson's (1982) distribution map shows *O. fragilis* along the east coast of Vancouver Island to approximately Campbell River. The most northern of the coastal herbarium records of *O. fragilis* is from Mitlenatch Island, British Columbia (*J.A. Calder & K.T. MacKay 30484* (14 June 1961) DAO-82236), at

49°57′N, which is at the confluence of Johnstone Strait and the Strait of Georgia, just east-southeast of Campbell River. Thus, while people have speculated about *O. fragilis* in coastal Alaska (see Benson's quote, above), the Yukon (Bernshaw and Bernshaw 1984), and even north of the Arctic Circle (Brethauer 2000), its occurrence in those places seems extremely unlikely.

It is important to correctly identify northern range limits so that they can provide crucial data for studies on climate change. There have been several studies using museum records of both plants and animals testing whether species have extended their ranges or altered their reproductive timing (phenology) in the face of warmer temperatures (e.g., Angert et al. 2011; Chen et al. 2011; Buizer et al. 2012; Panchen et al. 2012; Walker et al. 2012; Fisichelli et al. 2014). An error of either 205 km or 223 km in species range may not be huge for a bird or whale that can travel quickly. But for a diminutive cactus such as *Opuntia fragilis*, a range error of more than 200 km could falsely indicate that this species range is not affected by climate change. The range limit of *O. fragilis*, in particular, and cacti, in general, may eventually extend farther north with global climate change, but the current baseline for the range limit of *O. fragilis* should be 56°17′N.

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NEW AND INTERESTING SPECIES OF *GEMMABRYUM* J.R. SPENCE & H.P. RAMSAY (BRYACEAE, BRYOPSIDA) FROM CALIFORNIA AND THE WEST

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Abstract

Three species in the genus *Gemmabryum* J.R. Spence & H.P. Ramsay are described and illustrated. Two species, *G. brassicoides* J.R. Spence & K.M. Kellman and *G. vinosum* J.R. Spence & K.M. Kellman, are new to science. The third species, *G. californicum* (Sull.) J.R. Spence, previously considered to be part of *G. dichotomum* (Hedw.) J.R. Spence & H.P. Ramsay, is re-instated as a full species due to its highly unusual bulbil morphology. *Gemmabryum vinosum* is distributed in California, Oregon, and Montana, while the other two species are endemic to California.

Key Words: *Bryum*, California Floristic Province, *Gemmabryum brassicoides*, *Gemmabryum californicum*, *Gemmabryum vinosum*, mosses.

Recent fieldwork in California has revealed the presence of many new and interesting species in the Bryaceae. Two species, in *Imbribryum* Pedersen and *Ptychostomum* Hornschuch, have been described elsewhere (Spence and Shevock 2012, 2015). Among the remainder are several species in the genera *Gemmabryum* J.R. Spence & H.P. Ramsay, *Plagiobryoides* J.R. Spence, and *Rosulabryum* J.R. Spence. Within the genus *Gemmabryum* there are four undescribed species, two of which have been known about for several years with many collections made, and an additional two recently discovered species. In this paper we describe the two well-known new species of *Gemmabryum*, one of which appears to be endemic to California. We also describe and discuss an interesting species that has been previously ignored by earlier workers. These new species increase the described *Gemmabryum* flora of California to 17 (cf. Norris and Shevock 2004).

Gemmabryum was described for those species with stems not julaceous, heterogeneous laminal areolation, the presence of leaf axil bulbils and/or rhizoidal tubers, leaves typically lacking a limbidium, and small size (Spence and Ramsay 2005). The genus includes two groups, one consisting of the tuber-forming species centered around *G. subapiculatum* (Hampe) J.R. Spence & H.P. Ramsay, and the second consisting of the bulbil-forming species centered around *G. dichotomum* (Hedw.) J.R. Spence & H.P. Ramsay (=*G. bicolor* [Dickson] J.R. Spence). This latter group includes the type species *G. pachythecum* (Müll. Hal.) J.R. Spence & H.P. Ramsay. The distinctions between these groups are not always clear-cut, as a few species produce both bulbils and tubers, such as the pantropical *G. exile* (Dozy & Molk.) J.R. Spence & H.P. Ramsay. Also, a few species, which morphologically appear to belong to the bulbil-forming group, do not produce bulbils, at least in the wild, and occasionally produce rhizoidal tubers. The genus appears to be closest to *Bryum* Hedw. and *Imbribryum* Pedersen. Recent molecular work (Holyoak and Pedersen 2007) has suggested that *Gemmabryum* includes at least two major clades, corresponding to the bulbil- and tuber-forming groups. The tuber-forming clade may be phylogenetically closer to *Imbribryum* than it is to the bulbil-forming clade. In addition, Holyoak and Pedersen (2007) also determined that the large-tuber forming species *B. bornholmense* Wink. & R. Ruthe and *B. rubens* Mitt. were closest to *Rosulabryum capillare* (Hedw.) J.R. Spence, a placement supported by several additional morphological characters. Elsewhere, these two species have been transferred to *Rosulabryum* (Spence 2009). Until a more thorough molecular analysis including many more species in this group is available, we have retained the original concept of *Gemmabryum sensu* J.R. Spence and H.P. Ramsay (Spence and Ramsay, 2005), retaining within the genus the tuber-bearing species. One of the species discussed in this paper belongs to the bulbil-forming group that includes the type of the genus, while the other two cannot be easily assigned to either group.

Taxonomic Treatment

Gemmabryum brassicoides J.R. Spence & K.M. Kellman. sp. nov. (Fig. 1).—Type: USA,

FIG. 1. *Gemmabryum brassicoides* J.R. Spence & Kellman. 1. Fertile plant, dry. 2. Same, wet. 3–7. Leaves. 8–9. Leaf apices. 10. Mid-leaf cells at margin. 11. Mid-leaf cells. 12. Basal cells. 13. Exothecial cells at base of urn and stomata. 14. Mid-urn exothecial cells. 15. Exothecial cells at orifice, annulus, portion of peristome, and spores. (All from *Kellman & Shevock 5184*, isotype, KRAM). Scale bars: a – 1 mm (3–7); b – 100 µm (8–12); c – 100 µm (13–15); d – 1 mm (1–2).

California, Santa Cruz Co., Quail Hollow Ranch County Park, on vertical sandstone roadbank on the west side of Quail Hollow Rd across from the ranch buildings, live oak forest with ponderosa pine and chaparral, 18 Mar 2006, 160 m, 37°04′57N, 122°03′50W, *Kellman 5104* (holotype: CAS).

Plantae virides vel flavo-virentes, gemmiformes, foliis late ovatis, costa percurrenti vel in mucronem brevi-excurrenti, cellulis laminae distalibus parietibus crassis praeditis, structuris reproductivis peculiaribus asexualibus nullis; capsula cylindracea, peristomio perfecto.

Plants small, to three mm tall, short-rosulate, sometimes in annual comal tufts, rarely evenly foliate, with the apical coma ovoid or spherical. Stems with distinct central strand, sclerodermis 1–2 cells thick with red cell walls, sparsely rhizomatous, rhizoids brown. Leaves 0.55–0.78 × 0.42–0.54 mm, ca. 1.25:1; tightly appressed both wet and dry, broadly ovate, somewhat concave. Apex broadly obtuse to acute-mucronate. Margins weakly reflexed in proximal half, entire, without a border of differentiated cells. Costa subpercurrent to excurrent into a mucro, sometimes spurred or branched near the apex. In section at midleaf elliptical, not particularly prominent on either surface, with two guide cells on the ventral surface only, a central stereid band, and a dorsal epidermis of enlarged cells. Distal laminal cells with yellowish, moderately thick walls, at least in the outer comal leaves, hexagonal 2–3(4):1, 40–56 × 14–25 μm. Proximal laminal cells quadrate to short rectangular 1–1.5(2):1, 20–30 × 18–22 μm. Asexual reproductive structures not seen. Sexuality polyoicous. Gametangia terminal, leaves similar to vegetative leaves although somewhat smaller. Seta 8–11 mm, pale red to yellow with age, smooth throughout. Capsule horizontal to nodding, dark red when mature, cylindrical, 1.8–2.2 mm long, neck about ⅓ the total length, slightly wrinkled when dry. Exothecial cells irregular, irregularly quadrate at the mouth with thick red walls, stomata restricted to the neck. Operculum short conical. Exostome narrowly triangular, filiform at the apex, pale orange, finely papillose, trabeculae prominent. Endostomoe hyaline, basally united for ½ the length, with or without perforations, gradually and irregularly reduced to unornamneted filaments, cilia absent. Spores 10–14 μm, smooth, with an easily visible large organelle.

Paratypes: USA, CALIFORNIA. **Contra Costa Co.**: Hills west of Vasco Rd about four miles west of Byron, 250 m, 37°48′00″N, 121°42′30″W, 19 Mar 1997, *Shevock, O'Brien & Jessup 15024* (CAS). **Fresno Co.**: Trimmer Springs Rd above Pine Flat Reservoir, 365 m, 36°53′00″N, 119°17′45″W, 25 Mar 1996, *Shevock, Norris & Barahona 13164* (CAS); Sierra National Forest, off Cripe Rd 0.65 mile from Peterson Mill Rd, 1090 m, 37°02′30″N, 119°21′15″W, 16 Mar 1997, *Shevock & York 14946* (CAS). **Madera Co.**: Co. Rd. 29 across from Eastman Lake Visitor Ctr., 150 m, 37°13′00″N, 119°58′30″W, 15 Mar 1997, *Shevock 14934* (CAS); USDA San Joaquin Experimental Range, 985 ft, 37°04′53″N, 119°43′44″W, 25 Mar 2009, *Shevock 32638* (CAS). **Monterey Co.**: Fort Hunter Liggett, the Palisades off the Gabilan Rd, 330 m, 35°52′N, 121°13′W, 10 Apr 2004, *Kellman et al. 3764* (CAS). **San Luis Obispo Co.**: Saucito Springs, Carrizo Plain about four miles south of Soda Lake, 2300 ft, 35°09′45″N, 119°53′30″W, 7 Feb 2001, *Laeger, Carter & Butterworth 677* (CAS). **Santa Barbara Co.**: Los Padres National Forest, off Stagecoach Rd below Cold Springs Arch Bridge, 425 m, 31°40′N, 119°50′W, 26 Mar 2006, *Norris & Hillyard 108820* (UC) and *Shevock 27868* (CAS); west of San Marcos Pass along West Camino Cielo Rd, 2900 ft, 34°30′07″N, 119°51′56″W, 26 Mar 2006, *Shevock, Norris & Spence 27885* (CAS). **Santa Cruz Co.**: Quail Hollow Quarry, 150 m, 37°05′N, 122°04′W, 18 Aug 1996, *Kellman 296* (CAS); Quail Hollow Ranch County Park, 195 m, 37°05′N, 122°03′W, 29 Apr 2000, *Kellman 953* (CAS); Hilton Meadow at the end of Lucilles Ct. off SR 236 north of Boulder Creek, 260 m, 37°08′N, 122°09′W, 8 Apr 2000, *Kellman 931 & 7183* (CAS); Doyle's Meadow off Hwy. 9, 0.75 mile north of Boulder Creek bridge, 175 m, 37°08′N, 122°07′W, 15 Oct 2000, *Kellman 1154* (CAS). **Solano Co.**: Indian Spring two miles north of Rockville off Rockville Rd, elevation and lat-long not given, 27 Feb 1975, *Weber 48291* (COLO). **Tulare Co.**: Generals Hwy near entrance station above Three Rivers near Sycamore Creek, 440 m, 36°29′00″N, 118°50′15″W, 4 Apr 1998, *Shevock & Whitmarsh 16992* (CAS).

Habitat and Ecology

Forming turfs on sandstone walls near the coast, and rarely on metamorphic rock and granite in the interior, on outcrops in chaparral and ponderosa pine parkland, or in the transition between chaparral and oak woodland, to 400 m in elevation, and endemic to California. The plant grows in generally sunny locations where the substrate is moist in winter, but dry in the summer.

Associated bryophytes are *Cephaloziella divaricata* (Sm.) Schiffn and *Grimmia trichophylla* Grev.

Etymology

The name derives from the general look of the plants in the field similar to a tiny head of cabbage (*Brassica oleracea* L.).

Discussion

The only other *Gemmabryum* with leaves that remains erect-appressed wet or dry is *G. californicum.* If capsules are present, separation is easy, as *G. brassicoides* has cylindrical capsules, and *G. californicum* has short-ovoid capsules. Without capsules, or gemmae, the identification becomes more difficult and in certain cases nearly impossible. *Gemmabryum californicum* has distal laminal cells that are sometimes thick walled, but often have thin walls, whereas *G. brassicoides* distal laminal cells are always thick walled. A more subtle difference is in the shape of the terminal coma, with *G. brassicoides* being more commonly spherical but occasionally ovoid, while *G. californicum* is more commonly ovoid, but rarely spherical. Thus, if the apex of the plant is bluntly rounded, it is more likely *G. brassicoides.*

There are several interesting and unusual features regarding this species. First, it is common in lowland fire-adapted chaparral communities, and appears to be able to survive at least some fires. Secondly, it was originally thought to be dioicous like most other species of *Gemmabryum*, but male plants were not known. Recent laboratory studies (L. Stark, pers. com.) have revealed that at least the cultivated material of *G. brassicoides* is polyoicous, with synoicous, male and female shoots, which is extremely rare in the genus. Field collections need to be made to determine whether the species is typically mixed in populations and what environmental variables are associated with sex expression.

Taxonomic Treatment

Gemmabryum vinosum J.R. Spence & K.M. Kellman. sp. nov. (Fig. 2).—Type: USA, California, Fresno Co., BLM San Joaquin River Gorge Management Area, along river via a 0.25 mi. trail from powerhouse and parking lot, R22E, T10S, section 10, NAD 83, 37°04′37″N, 119°33′43″W, 600 ft, 26 Mar 2009, *Shevock, Kellman & Lodder 32676* (holotype: CAS; isotypes: H, KRAM, MO, NY, UC).

Plantae quoad affinitatem ignotae, rubrae vel burgundiaco-vinosae, gemmiformes, saepe in caespitibus interruptis duobus vel pluribus, foliis ovatis, in aristam laevum, distaliter hyalinam excurrentibus, in statu sicco subdivertgentes, cellulis laminae distalibus saepe pallidus vel hyalinis, tuberibus rhizoidalibus interdum praesentibus, rubro-brunneis, sphaericis, capsula cylindrica, peristomio reducto, ciliis nullis.

Plants small, up to one cm tall, more or less rosulate, or with annual comal tufts, rarely evenly foliate, burgundy-red and somewhat shiny when dry, or rarely olive-green. Usually simple, but sometimes branched. Innovations gemmiform to rosulate. Stems with a distinct central strand. Rhizoids reddish-brown, papillose. Rhizoidal tubers rare, reddish brown, 70–140 μm in largest dimension, cells not protuberant. Stem leaves usually remote, lanceolate, gradually getting broader toward the apex. Comal leaves tightly appressed when dry, erect when moist; red throughout (especially in the outer leaves) or at the distal end of the leaf, ovate to obovate, 1.0–1.2 × 0 .6–0.7 mm. Axillary hairs of one basal short rectangular brown cell and 3–4 linear, hyaline cells. Distal laminal cells generally hexagonal, 60–76(90) × 20–24(26) μm, 2.5–4:1; moderately thick walled but not porose. Proximal laminal cells generally quadrate to short rectangular, 1–2:1. Costa strong, excurrent into a smooth to slightly denticulate awn that is proximally concolorous with the upper leaf, but apically paler and appearing straw colored or hyaline and somewhat divergent when dry; costa in section with a strong abaxial epidermis, a central stereid band, and a ventral epidermis, rarely with a single layer of guide cells and an angular opening similar to a degraded hydroid strand dorsal to the guide cells. Margins recurved in the basal half, plane above, entire throughout, marginal cells of similar length to interior cells, but narrower, forming a weak limbidium. Asexual reproduction by rhizoidal tubers. Sexual condition dioicous, seta red, smooth, 13 mm long. Capsule cylindrical, three mm long, nodding, red when mature, wrinkled when dry, neck thick, about equal to the theca. Exothecial cells generally elongate, irregularly shaped, becoming shorter toward the mouth. Stomates restricted to the neck. Operculum conical. Annulus of 2–3 layers of vertically elongated, shingled cells, the inner cells remaining on the capsule, the outer cells falling with the operculum. Exostome pale yellow granular but not papillose, about 0.3 mm long. Endostome hyaline, basally united for about ½ the length, segments fenestrate, cilia appendiculate total length equal to the exostome. Spores smooth, 12–16 μm in largest dimension.

Paratypes: USA, CALIFORNIA. **Butte Co.**: South Table Mountain, 1096 ft, 39°33′01″N, 121°32′52″W, 10 Apr 2003, *Ahart 10081* (CAS, CHSC), Table Mountain, 447 m, 26 Mar 2011, *Hutten 15296* (CAS); Bidwell Park, along creek at diversion dam site in open grassland with blue and valley oaks along Big Chico Creek, 120 m, 39°46′43″N, 121°44′57″W, 21 Apr 2006, *Norris & Shevock 108860 & 108855* (UC) and *Shevock & Norris 27901* (BOL, CAS, DUKE, KRAM, MO, NY, RSA, UBC, UC). **Colusa Co.**: On roadside bank off SR 16 northeast of Rumsey near mile marker 5.46, 200 m, 39°18′N 122°19′W, 21 Mar 2003, *Kellman 2739a* (CAS). **Contra Costa Co.**: Mt. Diablo State Park, below observation deck of Mt. Diablo Peak, 3800 ft, 37°52′55″N,

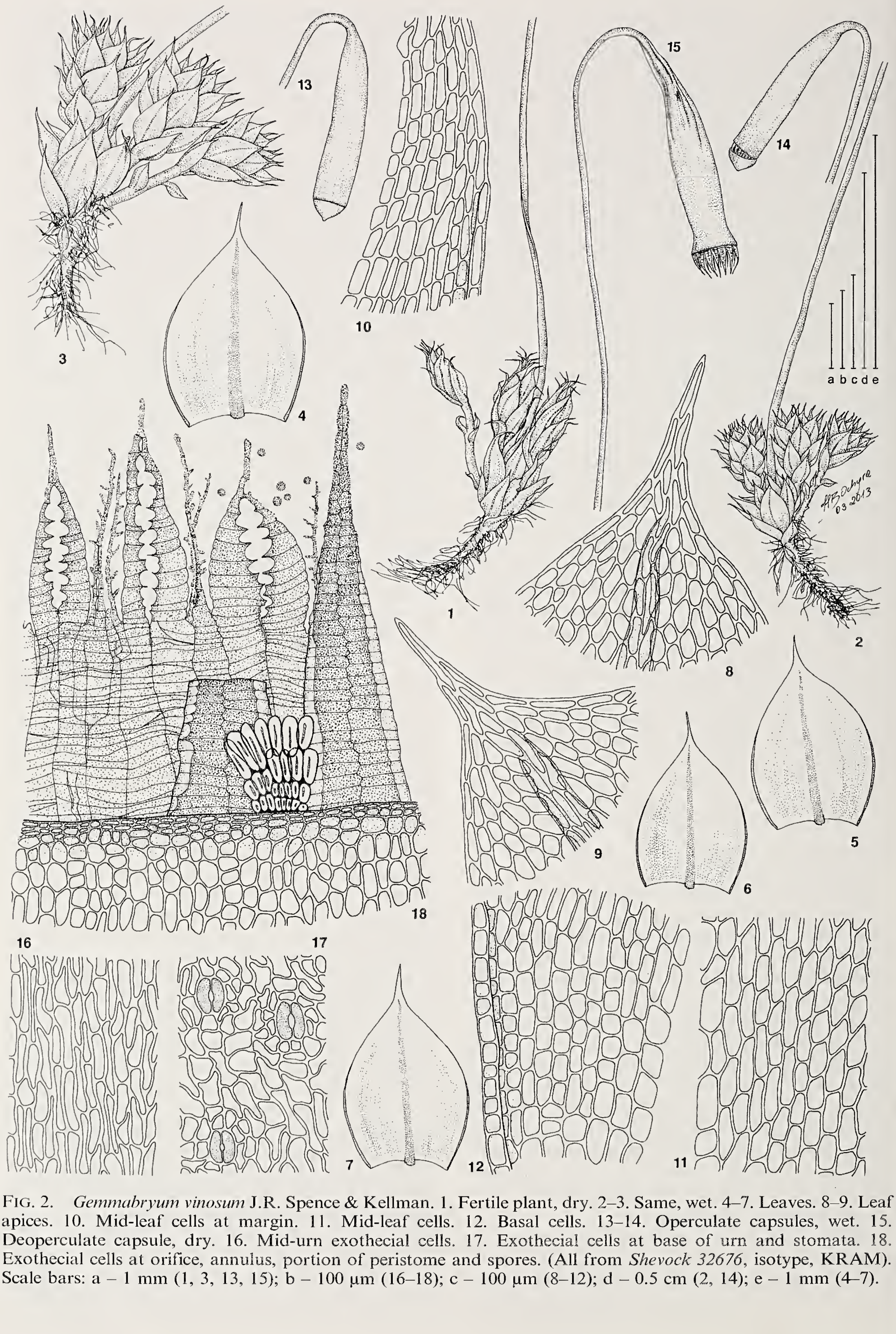

FIG. 2. *Gemmabryum vinosum* J.R. Spence & Kellman. 1. Fertile plant, dry. 2–3. Same, wet. 4–7. Leaves. 8–9. Leaf apices. 10. Mid-leaf cells at margin. 11. Mid-leaf cells. 12. Basal cells. 13–14. Operculate capsules, wet. 15. Deoperculate capsule, dry. 16. Mid-urn exothecial cells. 17. Exothecial cells at base of urn and stomata. 18. Exothecial cells at orifice, annulus, portion of peristome and spores. (All from *Shevock 32676*, isotype, KRAM). Scale bars: a – 1 mm (1, 3, 13, 15); b – 100 µm (16–18); c – 100 µm (8–12); d – 0.5 cm (2, 14); e – 1 mm (4–7).

121°52′55″W, 28 Feb 2004, *Shevock & Game 24635* (CAS); Flicker Ridge, 1035 ft, 37°49′52″N, 132°09′34″W, 1 Mar 2007, *Shevock et al. 29452* (CAS). **Fresno Co.**: from the type locality, *Hutten 14331* (CAS) and *Kellman, Shevock & Lodder 6087* (CAS); forest road 8S05 above the San Joaquin River, Sierra National Forest, 2500 ft, 37°12′25″N, 119°19′40″W, 21 Mar 2001, *Shevock & Norris 20633* (CAS), *Shevock & Norris 20642* (CAS, KRAM); Cripe Rd, Sierra National Forest, 3580 ft, 37°02′30″N, 119°21′15″W, 16 Mar 1997, *Shevock & York 14963* (CAS, MO, NY). **Kern Co.**: northern slopes of Cross Mtn. above Jawbone Canyon and Cottonwood Creek ca. six miles west of California Hwy 14, 1050 m, 35°17′30″N, 118°08′00″W, 21 Mar 1998, *Shevock, York & Hare 16913* (CAS). **Lake Co.**: Manning Creek where it nears Hwy 175 approximately four miles west of Lakeport, 445 m, 38°59′45″N, 122°56′32″W, 25 Mar 2002, *Kellman 2223* (CAS), and *Shevock & Mishler 21925* (CAS); along Hwy 53 about one mile south of Hwy 20, 1650 ft, 3 Apr 1976, *Norris 47656* (UC); Morgan Valley Rd, 1300 ft, 38°54′00″N, 122°35′00″W, 3 May 2004, *Toren 9331* (CAS); south base of Elk Mountain, Mendocino National Forest, 1500 ft, 39°15′35″N, 122°15′35″W, 21 Feb 2005, *Toren 9352a* (CAS); Harrington Flat Rd east of Boggs Lake and south of Mt. Hannah, 3000 ft, 38°52′15″N, 122°45′33″W, 17 Apr 2005, *Toren & Dearing 9399* (CAS); south bank of Eel River below forest road M1 and Logan Spring, 1800 ft, 39°24′30″N, 122°58′20″W, 19 Jun 2013, *Toren & Dearing 10087a* (CAS, DUKE, MO, NY). **Madera Co.**: Eastman Lake Visitor Center, 500 ft, 37°13′00″N, 119°58′30″W, 15 Mar 1997, *Shevock 14934a* (CAS); USDA San Joaquin Experiment Range, 985 ft, 37°04′53″N, 119°43′44″W, 25 Mar 2009, *Shevock 32635* (CAS, MO, NY) and *Hutten 14303* (CAS); Nelder Redwood Grove, Sierra National Forest, 4950 ft, 37°25′31″N, 119°34′22″W, 1 Jul 2013, *Shevock & Ma 42700* (CAS); slopes at south end of Bass Lake Recreation Area, Sierra National Forest, 3275 ft, 37°16′59″N, 119°32′07″W, 24 Mar 2009, *Shevock, Norris & Hillyard 32627* (CAS, CONN, F, HO). **Mariposa Co.**: Yosemite Valley, Yosemite National Park, 1280 m, 26 Aug 1966, *Flowers 6582* (COLO); Devils Gulch, South Fork Merced River, Sierra National Forest, 2000 ft, 18 Apr 2010, *Hutten 14911* (CAS), and *Hutten 14922* (CAS); BLM Merced River Wild & Scenic River Area, Hwy 140 at Slate Creek Bridge, 1440 ft, 37°38′05″N, 119°56′02″W, 6 Apr 2013, *Shevock & Dalton 41988* (CAS); slopes above Merced River along Moss Creek, Stanislaus National Forest, 2280 ft, 37°40′38″N, 119°48′21″W, 10 Apr 2010, *Shevock, Colwell & Hutten 34822* (CAS, KUN, VBGI) & *Hutten 15334* (CAS); slope above Rancheria Flat, 1815 ft, 37°40′18″N, 119°48′27″W, 3 Apr 2011, *Shevock & Hutten 37612* (CAS); along Hwy 140 at Merced River Bridge, El Portal, 1815 ft, 37°40′18″N, 119°47′38″W, 3 Apr 2011, *Shevock & Hutten 37643* (CAS, MO, NY); Yosemite National Park, Foresta Rd just south of Rancheria Flat, 1770 ft, 37°40′10″N, 119°48′31″W, 3 Apr 2011, *Shevock & Hutten 37647* (CAS, MO, NY). **Mendocino Co.**: south end of Black Butte River Bridge, 2680 ft, 39°47′58″N, 123°04′34″W, 21 Oct 1998, *Harpel & Toren 18654* (CAS). **Monterey Co.**: Zmudowski State Beach dunes, 5 m, 36°50′24″N, 121°48′13″W, 15 March 2009, *Kellman & Lodder 6032* (CAS); Los Padres National Forest off Indians Rd, 715 m, 36°30′30″N, 121°27′49″W, 3 Apr 2004, *Kellman 3676* (CAS); near Canogas Falls south of Devils Creek Canyon, 500 m, 36°04′12″N, 121°33′14″W, 25 Mar 2006, *Kellman & Shevock 5018* (CAS); Wagon Caves, 1500 ft, 36°05′00″N, 121°24′05″W, 22 Mar 2004, *Shevock, Dearing & Game 24740* (CAS); south of Santa Lucia Memorial Park, 2325 ft, 36°06′32″N, 121°27′43″W, 3 Apr 2004, *Shevock & Kellman 24801* (CAS). **Nevada Co.**: Spenceville Wildlife Management Area, 400 ft, 39°07′05″N, 121°15′39″W, 4 May 2005, *Ahart 11586* (CAS, CHSC); Tahoe National Forest, near the south fork of the Yuba River at the Golden Quartz picnic area about five miles east of Washington, 800 m, 39°21′N, 120°44′W, 10 Sep 2001, *Norris & Hillyard 102889* (UC). **Plumas Co.**: Plumas National Forest, Mt. Hough Rd, 30 Mar 2004, *Dillingham 1394* (CAS). **San Benito Co.**: Pinnacles National Monument, 435 m, 36°29′10″N 121°12′12″W, 5 Mar 2005, *Kellman, Shevock & Villasenor 4242* (CAS) and *Shevock, Kellman & Villasenor 26346* (CAS); Balconies Trail, 1550 ft, 36°29′53″N, 121°12′18″W, 12 Feb 2005, *Shevock & Hurley 26296* (CAS). **San Diego Co.**: along Hwy 94, ¾ mile northeast of Dulzura, 275 m, 32°39′09″N, 116°47′27″W, 24 Mar 2013, *Kellman & Lodder 7098* (CAS); Balboa Park, 81 m, 32.73504°N, 117.15822°W, 5 Mar 2013, *Marshall 1172* (CAS), *Marshall 1174* (CAS), *Marshall 1177* (CAS, SD). **San Luis Obispo Co.**: in open oak forest along Pozo Rd ca 1.5 miles west of Hwy 178 at La Panza Ranch, 490 m, 35°22′N, 120°12′W, 27 Dec 1979, *Norris 55145* (UC). **San Mateo Co.** On wood roof of garage, Los Altos Hills, 18 May 1983, *W.B. Shofield 81394* (private herbarium of JR Spence); **Santa Clara Co.**: near Pacheco Creek at Hole in the Rock just west of Kaiser-Aetna Rd in Henry Coe State Park, 240 m, 37°07′N, 121°22′W, 19 Apr 1998, *Whittemore & Briggs 6619* (CAS, MO). **Shasta Co.**: along Pit River at Potem Falls northwest of round Mountain, 400 m, 40°50′N, 122°00′W, 2 May 1991, *Norris 76355* (UC); Whiskeytown National Recreation Area along Clear Creek, 950 ft, 40°35′05″N, 122°32′59″W, 23 Mar 2003, *Shevock, Toren & Dearing 23847* (CAS). **Stanislaus Co.**: Henry Coe State Park, southern part of the

Orestimba Creek trail on the north side, 410 m, 37°11′N, 121°24′W, 18 Apr 1998, *Whittemore & Brigs 6591* (CAS, MO). **Tehama Co.**: Antelope Creek Canyon near the microwave station ca 10 miles east of Red Bluff on Bell Mill Rd, 210 m, 19 Jan 1971, *Berti 419b* (UC). **Tulare Co.**: Kaweah River below confluence with South Fork Kaweah River, 800 ft, 36°25′00″N, 118°55′00″W, 13 Apr 1999, *Shevock 17856* (CAS); along Shepard Peak Rd, 2000 ft, 36°29′30″N, 118°50′30″W, *Shevock & Whitmarsh 17019* (CAS); Sequoia National Park, off of Generals Hwy near Ash Mountain Headquarters, 490 m, 36°29′N, 118°49′W, 4 Apr 1998, *Shevock & Whitmarsh 17029* (CAS); Kern River near confluence of South Fork Creek, Sequoia National Forest, 3800 ft, 35°58′00″N, 118°29′09″W, 26 Apr 2002, *Shevock, Laeger & Carter 22080* (CAS, DUKE, H, KRAM, RSA, UBC); Bear Creek Rd below Mt. Home State Forest, 5200 ft, 36°11′15″N, 118°43′30″W, 27 Mar 1996, *Shevock, Norrris & Barahona 13204* (CAS); Terminus Reservoir near Three Rivers, 700 ft, 36°24′00″N, 118°59′00″W, 20 Mar 1998, *Shevock & York 16902* (CAS). **Tuolumne Co.**: Mather Rd west of Abernathy Meadow, 4365 ft, 37°52′21″N, 119°54′47″W, 25 Apr 2010, *Shevock, Colwell & Haas 34875* (CAS); South Fork Tuolumne River off Hwy 120 at Rainbow Pool, 2750 ft, 37°49′15″N, 120°00′46″W, 6 Apr 2013, *Shevock & Dalton 42007* (CAS); Stanislaus National Forest, Tuolumne Wild & Scenic River at junction with Clavey River, 1060 ft, 37°53′01″N, 120°09′12″W, 5 Aug 2011, *Shevock, Hutten & Haas 38582* (CAS, KRAM); between Indian Creek and Big Creek, 920 ft, 37°53′47″N, 120°12′58″W, 6 Aug 2011, *Shevock, Hutten & Haas 38597* (CAS); Sonnet Mine, 2955 ft, 1 Aug 2007, *Willits 232* (CAS). **Yuba Co.**: Daugherty Hill Wildlife Area about four miles NE of Loma Rica, 796 ft, 39°20′40″N, 121°21′52″W, 28 Feb 2005, *Ahart 11558* (CAS, CHSC). USA, MONTANA. **Lincoln Co.**: near Airport Rd in Tobacco Valley, 800 m, 48°56′N, 115°05′W, 7 Apr 2000, *Spribille 9695* (private herbarium of JR Spence). USA, OREGON. **Wasco Co.**: near Rte 218 just west of Clarno, 405 m, 44°54′N, 120°28′W, 23 Mar 2008, *Kellman & Shevock 5779* (CAS); Memaloose State Park, north of a rest area along I-84 east of Mosier, 45 m, 45°41′N, 121°20′W, 27 Mar 2008, *Kellman & Shevock 5849* (CAS). **Wheeler Co.**: above Hwy 218 between mile markers 31 & 32, east of Clarno unit of John Day National Monument, 650 m, 44°54′N, 120°19′W, 23 Mar 2008, *Shevock & Kellman 31604* (CAS).

Distribution and Ecology

Forming turfs on acidic rock, often granite or basalt, rarely on sandstone, or on soil, in generally sunny locations, in grasslands, chaparral and open conifer-oak forests, below 1500 m, usually away from the influence of maritime fog, primarily Californian but also known from Oregon and Montana.

Associated bryophytes are *Didymodon nicholsonii* Culm., *Grimmia laevigata* (Brid.) Brid., and *G. trichophylla* Grev.

Etymology

The name derives from the wine purple color of the plants including the leaves and stems.

Discussion

Gemmabryum vinosum is easily recognized in the field by its burgundy colored leaves with the lighter colored awns diverging from the apex. The plants do have a certain shininess, but not the metallic iridescence of *Imbribryum alpinum* (With.) Pedersen or *Pohlia cruda* (Hedw.) Lindb. It has a scattered distribution in the drier portions of the West, and it is so distinctive that it is surprising that it has not been described previously.

Several collections have shown bulbil-like buds produced singly in the leaf axils of the coma. These buds appear to be incipient innovations, but in the two plants where they have been seen, there were no perichaetia or perigonia present. Furthermore, it is not clear that the buds have clear excision mechanisms — all have remained attached to the stem during dissection, and there does seem to be a progression of growth. The smallest buds are spherical with leaf primordial similar to those of *Gemmabryum barnesii* (Wood) J.R. Spence. Larger buds have similar leaf primordia, but the basal portion of the bud extends like a stem elongation, as found in *G. caespiticium* (Hedw.) J.R. Spence. Even larger buds have tiny leaves complete with the awns of the adult leaves. It is possible that these innovations are finally released, because on several plants we have seen short plants with rhizoids, clustered around, but not attached to the lower stem of the main plant.

Gemmabryum vinosum has been confused with sterile material of *Rosulabryum erythroloma* (Kindb.) J.R. Spence, but can be distinguished by leaves imbricate and appressed when dry (vs. leaves twisted or contorted when dry in *R. erythroloma*), costa excurrent into the awn (vs. costa variable and often ending before the apex in *R. erythroloma*), leaves with only a weak border (vs. leaves with a distinct limbidium in *R. erythroloma*). Fertile material of *R. erythroloma* is also strongly rosulate. The species differs from *Imbribryum miniatum* (Lesq.) J.R. Spence by the rosulate plants (vs. plants julaceous in *I. miniatum*), presence of hairpoint (vs. apex obtuse in *I. miniatum*), and the upper cells more or less

parallel to the costa (vs. upper cells divergent from the costa in *I. miniatum*). *Rosulabryum gemmascens* (Kindb.) J.R. Spence produces slender innovations of ovate awned leaves, which are often reddish, and was thus confused with *G. vinosum* by Spence (1988). However, the awn of the innovation leaves is usually colored, while fertile *R. gemmascens* also has rosulate obovate leaves and a cylindrical capsule with a well-developed peristome.

Taxonomic Treatment

Gemmabryum californicum (Sullivant) J.R. Spence, Phytologia 89: 111. 2007, (Fig. 3). *Bryum californicum* Sull. Exploration and Surveys for a Railroad Route from the Mississippi River to the Pacific Ocean, Description of the Mosses and Liverworts 4(5): 188. 6. 1856.—Type: USA, California, Whipple Survey, 25 April 1854, *J. M. Bigelow* s.n. (FH!).

Described by Sullivant (1856) for material collected in California, this species was sunk into synonymy under *G. dichotomum* (as *Bryum bicolor* Dicks.) by early workers (see below). However, collections of some material labeled as *G. dichotomum* showed very unusual features, including extremely small and abundant propagula in the upper leaf axils. Our studies have shown this material to be very similar to the type and distinct from others in the complex. Below we provide the first detailed descriptions of this fascinating species.

Plants very small, up to five mm tall, but usually around one mm tall, sometimes evenly foliate below the ovoid terminal tuft, but more commonly ovoid gemmiform or barely foliate below the ovoid terminal tuft, golden green. Branched, or more commonly simple. Leaves tightly appressed both wet and dry, ovate, concave, 0.6–0.8 × 0.6–0.7 mm. Margins erect and unbordered, entire. Costa single, straight and without spurs, percurrent in a short apiculus, approximately 50 μm wide at the base and not much tapered above. Distal laminal cells irregularly hexagonal, 2–4:1, 30–46 × 10–14 μm, sometimes with thick walls. Proximal laminal cells short rectangular to quadrate, 1–1.5:1, not differentiated at the margin. Asexual reproductive bodies numerous, variously shaped (often obconical), multicellular gemmae produced in leaf axils and eventually obscuring the plant. Gemmae often massed around the plant. Rhizoidal tubers not seen. Sexual condition dioicous. Seta smooth throughout, pale at the base and getting progressively redder above, up to 15 mm long. Capsules variable from horizontal to suberect, deep red, short ovoid to short cylindric, merely wrinkled when dry, usually bulging in the middle with a thick and somewhat wrinkled neck roughly the same diameter as the mouth, 1–1.7 mm long. Stomata restricted to the neck. Operculum short conic. Annulus revoluble. Exostome teeth narrowly triangular with a somewhat long-acuminate apex, orange at the base and hyaline above; variably roughened. Endostome united in the basal half, segments very irregular in shape, about or slightly shorter than the exostome, hyaline, cilia absent. Exothecial cells very irregularly shaped, longitudinally or transversely elongated, with thick red walls. Spores 11–15 μm in diameter, smooth or slightly roughened, with an easily visible, large organelle.

Other specimens examined: USA, CALIFORNIA. **Butte Co.**: Bidwell Park, 21 April 2006, *Shevock & Norris 27908* (CAS). **Monterey Co.**: Carmel Valley Rd, 290 m, 36°16′37″N, 121°27′12″W, 2 Aug 2003, *Kellman 3099* (CAS); near junction of Gigling Rd and 8th Avenue, Fort Ord, 105 m, 36°38′35″N, 121°47′17″W, 22 Jan 2006, *Kellman 4186* (CAS); one road bank along Robinson Canyon Rd approximately five miles from the bridge over the Carmel River, 450 m, 36°28′N, 121°48′W, 11 Mar 2007, *Kellman 5303* (CAS); above SR198 approximately 1.5 miles east of San Lucas, 145 m, 36°08′N, 121°00′W, 17 Feb 2008, *Kellman 5708* (CAS); Ventana Wilderness, Los Padres National Forest, Arroyo Seco Trail, 700 m, 36°07′00″N, 121°28′31″W, 3 Feb 2007, *Kellman & Shevock 5226* (CAS); Robinson Canyon Rd 4.3 miles from the bridge over the Carmel River, 1 415 m, 36°28′N, 121°48′W, 9 Feb 2007, *Kellman & Shevock 5263* (CAS); road bank along Robinson Canyon Rd 3.7 miles from the bridge over the Carmel River, 330 m, 36°29′N, 121°48′W, 19 Feb 2007, *Kellman & Shevock 5270* (CAS). **Santa Cruz Co.**: small plateau above the Scotts Valley High School, south exposure, 250 m, 37°04′21″N, 122°00′31″W, 10 Mar 2001, *Kellman 1350* (CAS); Cupcake Hill behind Scotts Valley High School off Glenwood Drive, 245 m, 37°04′21″N, 122°00′32″W, 27 Aug 2008, *Kellman 5861* (CAS); Big Basin State Park, below Basin Trail and China Grade Rd, 685 m, 37°12′41″N, 122°12′43″W, 20 Jul 2008, *Kellman 5875* (CAS); Hwy 9 near mile marker 22.6 between Boulder Creek and Hwy 35, 500 m, 37°13′40″N, 122°08′58″W, 24 Jan 2009, *Kellman 5990* (CAS, MO, NY, UC). **Tuolumne Co.**: along Hwy 108, 6.1 miles east of Mi-Wok Ranger Station, 1675 m, 38°08′N, 120°05′W, 6 Sep 1999, *Shevock 18584* (CAS).

Distribution and Ecology

Widely scattered to forming dense turfs on sunny sandstone or rarely volcanic rock or thin soil over rock, sometimes in sandy sites, in open vegetation or open oak-pine forests, ≤1000 m, endemic to California.

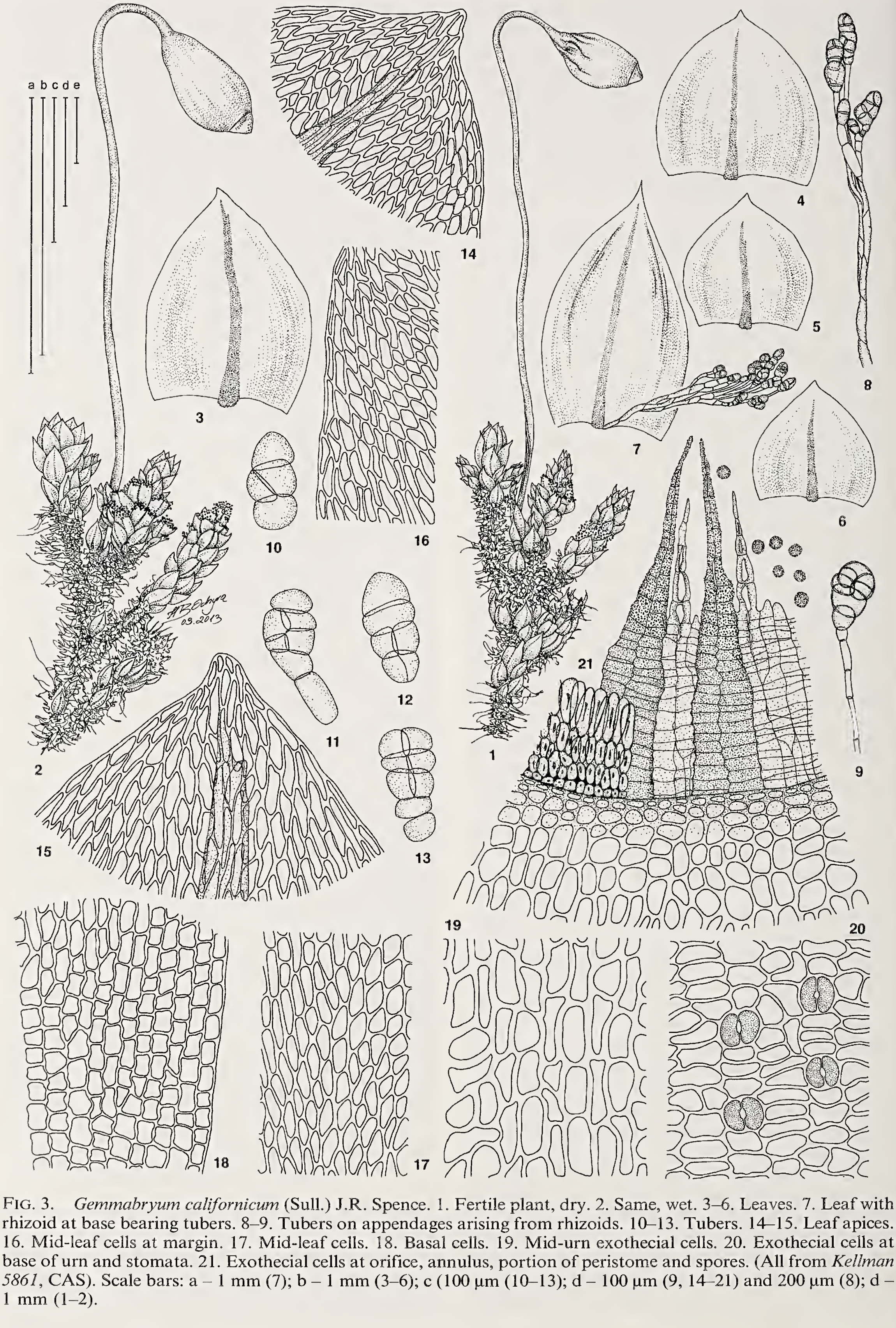

FIG. 3. *Gemmabryum californicum* (Sull.) J.R. Spence. 1. Fertile plant, dry. 2. Same, wet. 3–6. Leaves. 7. Leaf with rhizoid at base bearing tubers. 8–9. Tubers on appendages arising from rhizoids. 10–13. Tubers. 14–15. Leaf apices. 16. Mid-leaf cells at margin. 17. Mid-leaf cells. 18. Basal cells. 19. Mid-urn exothecial cells. 20. Exothecial cells at base of urn and stomata. 21. Exothecial cells at orifice, annulus, portion of peristome and spores. (All from *Kellman 5861*, CAS). Scale bars: a – 1 mm (7); b – 1 mm (3–6); c (100 μm (10–13); d – 100 μm (9, 14–21) and 200 μm (8); d – 1 mm (1–2).

Associated bryophytes are *Didymodon brachyphyllus* (Sull. in Whipple) Zand. *Cephaloziella divaricata* (Sm.) Schiffn., and *Rosulabryum canariense* (Bridel) Ochyra.

Discussion

Gemmabryum californicum can be recognized from the following combination of characteristics: golden-brown leaves that are tightly appressed in comal tufts either wet or dry, short ovoid capsules, and the common presence of irregularly shaped, multicellular gemmae produced in the leaf axils. It can only be confused with *G. brassicoides*. To separate these two plants, see notes in the discussion under *G. brassicoides*.

Originally, we thought to describe *G. californicum* as a new species, especially with the discovery of the gemmae, unique in *Bryum* sensu lato. However, because the type specimen of *Bryum californicum*, which has no gemmae, but otherwise strongly resembles the plants with capsules and gemmae, it became clear that the only prudent course of action is to label the gemmiferous plants *G. californicum*, instead of creating a new name.

There has been some controversy about the status of *Bryum californicum* since it was first described. Kindberg (1897) thought that it was a subspecies of *Bryum atropurpureum* (Bruch. & Schimp.), a taxon that was later synonymized with *Bryum bicolor* Dicks. by Corley et al. (1981). Many present day authorities (Ochi 1980, 1985; Allen 2002; Anderson, Crum and Buck 1990; Iwatzuki 1991; Ignatov and Efonina 1992) feel that the proper name for *B. bicolo*r is *B. dichotomum*. Podpera (1956) followed Corley et al., and made the new combination *Bryum bicolor* subsp. *californicum*. Whether or not you choose *bicolor* or *dichotomum* (the latter epithet for BFNA), that taxon is known by its large axillary bulbils with leaf primordia in the upper third of the bulbil.

This confusion can easily be attributed to the type specimen at Farlow Herbarium (FH) and ultimately to Sullivant's liberal concept of *Bryum californicum*. There are three specimens attached to the card with the type, all from Herbarium Sullivant. One is labeled as the type specimen with the following information on the label: California, Whipple Survey J. M. Bigelow, 25 April 1854. This plant matches the drawing and description in Sullivant's paper.

The second collection was made by Bolander, with no date or location other than California. This plant has leaves that are not appressed at the apex like the type, but is similar in areolation and sporophyte. The third collection has a typed label enclosed that reads: Collected in Southern California (between 32° and 36°N. lat. and 114° and 121°W. long.) on the Mexican Boundary Survey; by C. C. Parry, under the direction of Maj. W. H. Emory, Chief astronomer of the Commission. The outer label adds the years 1849–52. This third collection has only short capsules in common with the type specimen, as the leaves are not at all appressed to the stem, and are more like a *Ptychostomum* or narrow leaved *Rosulabryum*. Apparently Sullivant was willing to place any *Bryum* with a short capsule under the name *californicum*. It is the authors' opinion that only the type specimen is actually *G. californicum*, albeit without the gemmae.

Nonetheless, the earlier synonymies require that we defend separation from *Bryum dichotomum*. As stated above, that taxon has short capsules very similar to *G. californicum*. However, the bulbils from that plant are very large and complex (Vanderpoorten and Zartman 2002). The gemmae from *G. californicum* are hardly organized beyond an obclavoid conglomeration of cells. Moreover, in *Bryum dichotomum*, the leaves, that may be appressed when dry in some forms, always relax somewhat when wet. This is not the case in *G. californicum*, where the leaves are in tight comal tufts wet or dry.

We believe that the axillary gemmae of *G. californicum* are actually neotonous forms of the bulbils in the *Bryum dichotomu*m complex. Although no controlled growth experiments have been done for confirmation, observation of plants in the field seem to indicate that gemmae growth can be so explosive that it forces the apex of plant to fall off, exposing a rosette of remaining leaves surrounded by hundreds of gemmae.

Although currently considered endemic to California, the species should be sought for in coastal Mediterranean climate areas of Oregon, Washington, and British Columbia.

Conclusions

Fieldwork during the last 20 years has revealed many moss species new to science from the California Floristic Province. Within the traditional Bryaceae, the following species have been recently described (including in this paper): *Gemmabryum brassicoides*, *G. vinosum*, *Imbribryum torenii*, *Pohlia robertsonii*, *Haplodontium tehamense*, *Mielichhoferia shevockii*, and *Ptychostomum pacificum*. Additional undescribed species from California in *Anomobryum, Gemmabryum, Plagiobryoides,* and *Rosulabryum* are awaiting formal publication. Overall, at least 60 known species have been documented from California within the Bryaceae (excluding *Pohlia* and its relatives which have been recently placed in resurrected Mielichhoferiaceae for BFNA), representing almost 10% of the moss flora,

and making the state perhaps the most diverse in temperate Northern Hemisphere (Spence 2014).

With the recognition of three new species, California also becomes one of the two major centers of diversity in the Northern Hemisphere for *Gemmabryum* section *Gemmabryum*, with the other center being western and southern Europe. Including traditionally recognized species, there are now six known from the state, *G. barnesii*, *G. brassicoides*, *G. californicum*, *G. dichotomum* (=*G. bicolor*), *G. gemmiferum*, and *G. gemmilucens*. This section appears to be most diverse in Mediterranean-climate regions, at least in the Northern Hemisphere. Preliminary work (J.R. Spence unpublished) indicates that the Mediterranean-climate regions of Chile may also represent an important center of diversity.

Key to species of *Gemmabryum* section *Gemmabryum* in California

The following key includes all species of the section related to *G. dichotomum* found in California and also includes *G. vinosum*.

1. Plants lacking bulbils, producing tubers on rhizoids, shoots somewhat elongate, leaves not imbricate, often somewhat twisted or contorted when dry, if imbricate then rhizoidal tubers abundantly produced, small, spherical to pyrform, brown Section *Tuberibryum* [not in key; see Spence 2014]

1′. Plants with 1–many bulbils in axils of upper innovation leaves, shoots budlike or occasionally elongate, leaves imbricate, not contorted or twisted when dry; tubers rarely produced (strongly gemmiform plants lacking tubers and bulbils key here) 2

2. Plants with bulbils in upper leaf axils 3

2′. Plants lacking bulbils, even in absence of capsules 7

3. Bulbils large, (200) 300–750 μm, leafy primordia rising from near base or mid-bulbil, 1–2 per leaf axil. . . . . *Gemmabryum dichotomum*

3′. Bulbils smaller, (50)100–400 μm, leafy primordia from upper 1/3 of bulbil to short and peglike or primordia lacking, 1–25 or more per leaf axil 4

4. Bulbils small, 60–80 μm, key-hole shaped to obconical, cells in 2–4 tiers, numerous, often 100's. . . . . *Gemmabryum californicum*

4′. Bulbils larger, typically >100 μm, cylindrical to top-shaped or round, fewer 5

5. Bulbils small, 100–200 μm, round or cylindric, primordia lacking or very short and peg-like. . . . . *Gemmabryum gemmilucens*

5′. Bulbils mostly 150–350 μm, pyriform to conic, distinct primordia present 6

6. Bulbils 150–250 μm long, primordia narrow, acute and tooth-like . . . . *Gemmabryum gemmiferum*

6′. Bulbils mostly >200 μm, primordia broad, obtuse, leaf-like *Gemmabryum barnesii*

7. Leaves usually red, distal lamina often hyaline, costa strong, long excurrent, hairpoint colored, reddish, sometimes spinulose and hyaline at tip; rhizoidal tubers sometimes present . . . . *Gemmabryum vinosum*

7′. Leaves green, golden or yellow-green, distal lamina not hyaline, costa not reaching apex to short excurrent in stout colored point, not spinulose; tubers unknown . . . . *Gemmabryum brassicoides*

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The authors would like to thank Jim Shevock for help on the manuscript, and for his enthusiasm and support for our studies. David Toren provided many specimens and showed the senior author *G. vinosum* for the first time in the field. Halina Bednarek-Ochyra provided the excellent illustrations, for which we are extremely grateful. We thank the curators of Farlow Herbarium for the loan of the type of *G. californicum*.

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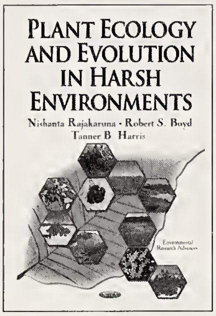
REVIEW



Plant ecology and evolution in harsh environments. By NISHANTA RAJAKARUNA, ROBERT S. BOYD, and TANNER B. HARRIS (EDS.). Nova Publishers, Hauppauge, NY. 426 pp. ISBN 97816332 19557. Price $250.00 (ebook).

Around the world, considerable plant diversity and endemism are hosted by environments in which plant productivity is sharply limited in some way. In many cases these special environments stand out as "islands" of unique, small-statured plants surrounded by seas of lusher, climatically determined vegetation. If it sounds to you like I am writing about Californian serpentines, there's a reason for that; our state is blessed with one of the world's best-studied special edaphic floras, about which many articles and several entire books have been written (including a few by me). However, Rajakaruna, Boyd, and Harris have set themselves the ambitious task of synthesizing current scientific knowledge about a much broader spectrum of harsh environments for plants: unusual bedrocks (gypsum, carbonate rocks, serpentine), saline soils, metal-contaminated settings, and even – to a relatively small extent – fire-prone and climatically challenging environments. The result is a wide-ranging collection of recent scientific work on how plants adapt to stress, and how stress shapes higher-order outcomes in evolution, ecology, and conservation.

Similarly to a recent edited volume on serpentine (Harrison and Rajakaruna 2011), and in contrast to several previous treatments of regional or global edaphic floras, the emphasis here is strongly on new scientific developments. Recent "-omics" techniques are being used to understand the physiological mechanisms by which plants and microbes adapt to various forms of stress, the genetics underlying these adaptations, and the phylogenetic relationships among adapted lineages; several chapters describe these techniques and the current status of the results. Some chapters focus on particular settings, such as gypsum soils or arctic-alpine climates, and provide multidisciplinary overviews of evolutionary-ecological research in these environments. Other chapters focus on particular taxonomic groups facing particular stresses, for example bryophytes in dry climates, lichens on metal soils, and the amazing genus *Mimulus* in its several extreme settings (copper mines, saline soils, serpentine). Still other chapters take a problem-centered approach, asking, for example, whether mycorrhizae play a special role on harsh soils, or whether plants on infertile soils face unique challenges with respect to conservation, restoration, and/or climate change.

Recurring questions throughout the book, well synthesized in the final chapter, include: is stress tolerance labile or conserved within lineages; are species tolerant through ecotypes or plasticity; is stress avoidance an alternative to tolerance; how does adaptation to one stress affect adaptation to another one; what role does stress adaptation play in the origin of new species? At the risk of partiality, one of my favorite chapters was Chapter 9 ("The Evolutionary Ecology and Genetics of Stress Resistance Syndrome Traits" by von Wettberg, Ray-Mukherjee, D'Adesky, Nesbeth, and Sistla), because it poses the theoretical question fundamental to this book – what is stress and is there a general way that plants adapt to it? – and brings to bear an impressive array of recent techniques to address, if not fully answer, this question. As in all scientific syntheses, the unresolved questions outnumber the neat take-home messages.

Readers beware: this is not a natural history book; it is a roadmap into the scientific literature rather than out into the field. It also necessarily leaves many subjects thinly covered. As one outstanding example, carbonate rock floras need more synthetic work, comparable to what's been done on gypsum and serpentine. Fire-prone and harsh climates as plant stresses both richly deserve 16-chapter edited volumes of their own. Nonetheless, anyone interested in how the world's more challenging terrestrial environments contribute to biological diversity will find much to enrich their knowledge in this book.

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